Using Vegetation to Assess Wetland Condition:

a multimetric approach for temporarily and seasonally flooded depressional wetlands and herbaceous-dominated intermittent and ephemeral riverine wetlands in the northwestern glaciated plains ecoregion, Montana

Prepared for:

Montana Department of Environmental Quality
and
U.S. Environmental Protection Agency

By:

W. Marc Jones

Montana Natural Heritage Program
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SUMMARY

The Montana Department of Environmental Quality is implementing a comprehensive wetland monitoring and assessment program to evaluate the condition of the state's wetlands. As part of this effort, the Montana Natural Heritage Program is developing site-level numerical vegetation biocriteria for wetlands. Assessing wetland condition by measuring the response of the biological community has been successfully demonstrated in many wetland systems using a variety of taxa. This study attempted to evaluate wetlands by measuring vegetation response to anthropogenic stressors for temporarily and seasonally flooded depressional and herbaceous-dominated intermittent and ephemeral riverine wetlands in the northwestern glaciated plains ecoregion in north-central Montana. Sample wetlands were ranked along a human disturbance gradient based on site- and local landscape-level factors. Vegetation attributes that changed predictably along this gradient were identified and combined into a multimetric index for each wetland type. These indices were significantly related to wetland condition, as measured by the human disturbance gradient, for both depressional and riverine wetlands. When wetlands were divided into three disturbance categories (reference condition, moderately disturbed, and severely disturbed), vegetation metrics were able to correctly classify 73% of depressional and 86% of riverine wetlands sampled. The multimetric index for depressional wetlands responded primarily to on-site agricultural disturbance and was comprised of four metrics: the floristic quality index and relative cover of native perennials, species with a coefficient of conservatism ≥ 4, and exotic species. The riverine multimetric index responded primarily to on-site grazing intensity and included the richness of native perennials, Simpson diversity index, proportionate richness of tolerant species, relative cover of intolerant species, and floristic quality index.

Another aspect of this study was to evaluate the effectiveness of classifying watersheds (5th-level U.S. Geological Survey hydrological units) into disturbance categories based on land use patterns. Watershed-scale disturbance categories showed no correlation with either wetland condition as measured by site-level and smaller-scale disturbance measures or vegetation metrics. Smaller-scale disturbance factors appear to be more important in determining condition of sampled wetlands in this study.

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INTRODUCTION

Wetlands are critically important systems that provide numerous biological and economic benefits, including groundwater recharge, filtration and storage of sediments, nutrients, and pollutants, and floodwater storage and attenuation, as well as providing habitat to numerous species across a broad array of taxa (Brinson et al. 1981, Keddy 2000, Hauer et al. 2002a, b). They are essential to the maintenance of regional biodiversity, and, in the case of riparian habitats, provide structural habitat diversity otherwise lacking in semi-arid areas (Patten 1998). Consequently, the significance of wetlands is disproportionate to their physical extent on the landscape, especially in semi-arid regions such as Montana (Finch and Ruggiero 1993, Patten 1998). Yet despite their importance to both humans and wildlife, an estimated 25% of Montana's wetlands have been lost since 1780 (Dahl 1990). Although in the last 30 years the number of regulatory and incentive-based wetland conservation programs has increased considerably, wetlands continue to be lost and degraded nationwide (U.S. EPA 1994, Dahl 2000, National Research Council 2001).

To improve wetland conservation in Montana, the Montana Department of Environmental Quality has initiated a comprehensive statewide wetland monitoring and assessment program. The goals of this program are to characterize the condition and extent of Montana's wetlands and to identify and document which anthropogenic stressors are most limiting to wetland health statewide and within regional watersheds. The implementation of this program will help prioritize statewide wetland conservation and restoration efforts. A component of this overall effort is to develop site-level numerical biocriteria for different wetland types within broad ecoregions across the state.

Biological assessments can be accurate and cost-effective tools to assess wetland condition and measure impairment (Karr and Chu 1999). Because biota integrate multiple physical and chemical parameters, directly measuring the biotic community's response to anthropogenic stressors can be the most direct means to evaluate the effect of those stressors on wetland condition and function (Danielson 2002). The utility of using biota to assess wetlands and streams has been demonstrated for various taxa, including fish, diatoms, benthic and terrestrial macroinvertebrates, birds, and vegetation (Karr 1991, DeKeyser 2000, Helgen and Gernes 2001, Kimberling et al. 2001, Mack 2001, Bryce et al. 2002, Fore and Grafe 2002, but see Heino et al. 2003, Tangen et al. 2003). The effectiveness of this method has already been demonstrated for perennial wetlands in Montana by Apfelbeck (2001), who developed biocriteria for diatoms and macroinvertebrates.

The purpose of this study was to use a multimetric approach (Karr and Chu 1999) to develop numerical vegetation biocriteria for depressional and riverine wetlands in the northwestern glaciated plains ecoregion in Montana. Many of the depressional and riverine wetlands in this ecoregion have a relatively brief inundation period in the spring and may be dry through most of the growing season. Therefore, plants were chosen as response taxa because vegetation is a good indicator of wetland condition and may be especially useful in wetlands that are only seasonally or ephemerally flooded. Plant species are diverse, have rapid growth rates, and respond directly to environmental change; additionally, it is easy to quantify shifts in plant community composition (Fennessy et al. 2002). Vegetation is also an important habitat variable for numerous invertebrate and vertebrate animals. Vegetation metrics, therefore, have the possibility of integrating wetland condition and wildlife habitat assessments.

METHODS

STUDY AREA

Geology and Climate

The study area encompassed the Middle Milk sub-basin (4^{th}-level U.S. Geological Survey hydrologic unit code 10050004) and adjoining areas (Figure 1). This region lies within Blaine, Hill, Phillips, and Valley Counties in north-central Montana. The area is part of the northwestern glaciated plains ecoregion (Woods et al. 1999) and is characterized by plains, terraces, floodplains, and morainal landforms formed in glacial till, gravel deposits, and alluvium over shale, clay shale, sandstone, and siltstone (Nesser et al. 1997). Most of the study area is underlain by the marine-origin shale and clay-shale of the Bearpaw and Claggett formations. Other geologic substrates include sandstone and sandy shale in the breaks along the Milk River and Quaternary-age alluvium in the valley bottom of the Milk River and its larger tributaries.

The region's climate is semi-arid and continental, with cold winters and warm summers. Mean temperatures range from –9.7ºC in January to 20.1ºC in July at Havre and from –14.2ºC in January to 18.6ºC in July at Opheim; mean annual precipitation at these stations is 291 mm and 303 mm, respectively (Western Regional Climate Center 2004). Most precipitation falls in late spring and early summer and occurs as steady, soaking frontal system rains. Summer rainfall comes mainly from convection thunderstorms that typically deliver bursts of intense rain in scattered locations. These storms are often accompanied by large-diameter hail and flashfloods. Where rainfall exceeds evapotranspiration, conditions are suitable for agriculture, particularly cereal grains.

The landscape is rolling prairie characterized by modest vertical relief. Elevations range from 600 m a.s.l. along the Milk River at Glasgow to 915 m a.s.l. near Opheim. The region's gentle topography is the product of past glacial scour and deposition. Much of the area is mantled by deposits of glacial till, outwash, and drift up to 30 m thick (Nesser et al. 1997).

Another aspect of semi-arid, continental climates is extreme year-to-year variability in precipitation. Severe drought conditions occur on average in two out of every ten years. Climate data from Redstone, Montana, which is comparable to the study area, indicate that one year in ten will have a total annual precipitation of less than 200 mm or more than 450 mm (Richardson and Hanson 1977).

Depressional Wetlands

Depressional wetlands, known as prairie potholes, occur throughout the study area but are most abundant north of the Milk River on gently rolling prairie terrain. Prairie potholes form in small, shallow depressions. These are primarily of glacial origin and many potholes were created when stranded ice blocks melted following glaciation. In the study area, these wetlands average less than 0.5 ha in size and are often only ephemerally flooded. Potholes flood seasonally in the spring to early summer and are sometimes inundated for as little as a few weeks in spring (Kantrud et al. 1989). Vegetation in these wetlands is primarily structured along a hydrological gradient. Plant communities occur as concentric zonal bands, depending on each zone's relative period of inundation (Johnson et al. 1987, van der Valk and Welling 1988). Drier, temporarily flooded potholes are dominated by western wheatgrass (*Pascopyrum smithii*) and needle spikerush (*Eleocharis acicu-*

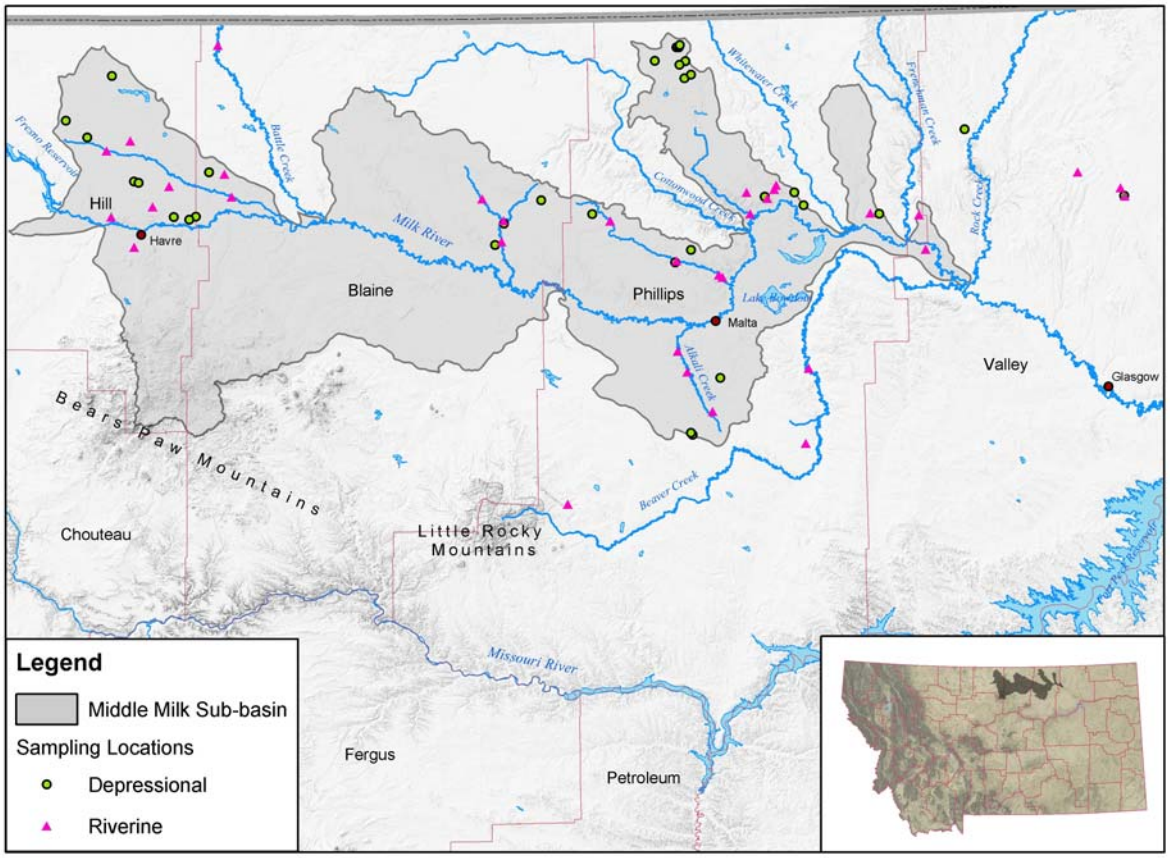

Figure 1. Study area and locations of sample wetlands.

laris). As the inundation period increases and wetlands become seasonally flooded, foxtail barley (*Hordeum jubatum*) and common spikerush (*Eleocharis palustris*) become dominant. Prairie potholes receiving saline groundwater inputs or that occur in more alkaline soils often support salt-tolerant species, such as Nuttall's alkaligrass (*Puccinellia nuttalliana*), saltgrass (*Distichlis spicata*), bearded sprangletop (*Leptochloa fusca* ssp. *fascicularis*), and common threesquare (*Schoenoplectus pungens*). Semipermanently flooded wetlands, which retain water into late summer and support hydrophytic vegetation, such as broadleaf cattail (*Typha latifolia*) and hardstem bulrush (*Schoenoplectus acutus*), are rare in the study area.

Riverine Wetlands

Riverine wetlands are extremely diverse across the study area. These systems encompass a wide range of natural variability and differ considerably depending on hydrology, geomorphology, and time since last flood disturbance. Riparian habitats range from oxbow marshes and cottonwood gallery forests along the Milk River and its larger perennial tributaries to mesic herbaceous-dominated communities along small, ephemeral drainages.

Study wetlands were confined to Milk River tributaries, which are generally small and often intermittent or ephemeral. Vegetation is often shrub- or herbaceous-dominated, although narrow, discontinuous bands of plains cottonwood (*Populus deltoides*), box-elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*) occur sporadically along floodplains and terraces. Depending on a site's hydrologic potential, channels and floodplains may be dominated by hydrophytic vegetation, such as Nebraska sedge (*Carex nebrascensis*), water sedge (*Carex aquatilis*), or common spikerush, or by mesic vegetation, such as western snowberry (*Symphoricarpos occidentalis*), Woods rose (*Rosa woodsii*), clustered field sedge (*Carex praegracilis*), tufted hairgrass (*Deschampsia caespitosa*), or western wheatgrass. Saltgrass, common threesquare, and black greasewood (*Sarcobatus vermiculatus*) are common along more alkaline streams. Terraces often support communities of silver sage (*Artemisia cana*) and western wheatgrass.

Upland Vegetation

The native upland vegetation is a mix of short- and mid-grass prairie communities intermixed with shrub steppe. Steppe vegetation is the result of a semi-arid continental climate: the highly variable precipitation favors shallow-rooted herbaceous perennial grasses and deep-rooted shrubs over forests or woodlands. Shrub steppe vegetation is characterized by open stands of silver sagebrush or Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) over an herbaceous layer dominated by western wheatgrass, blue grama (*Bouteloua gracilis*), or needle-and-thread (*Hesperostipa comata*). The co-occurrence of short- and mid-grass prairies is due to climatic variability. Shorter, drought-resistant grasses such as blue grama increase in abundance during times of drought, whereas mid-grasses, such as the rhizomatous western wheatgrass and the bunch-forming prairie junegrass (*Koeleria macrantha*) and needle-and-thread, increase under more favorable moisture conditions.

Study Design

Bioassessments and multimetric indices, such as indices of biological integrity (IBIs), are designed to detect the response of a biological community to human disturbance. Central to developing a multimetric index is sampling the target population (in this case depressional and riverine wetlands) across a human disturbance gradient (Teels and Adamus 2002). Two basic sample designs are available: probabilistic (e.g., stratified random) and targeted. Probabilistic designs are more powerful in that they allow inferences to be made from the sample population (i.e., sampled depressional wetlands) to the larger population of concern (i.e., all temporarily or seasonally flooded depressional wetlands within the study area). Thus probabilistic designs allow wetland condition to be characterized at a watershed scale and the proportion of wetlands that meet minimum aquatic life uses to be determined. Because of the greater inferential power of a probabilistic sample design, wetlands were initially sampled using the stratified random procedure described under the Watershed Ranking section below.

Unfortunately, a potential shortcoming in probabilistic designs is that the extremes of the human disturbance gradient will be under sampled (Danielson 2002). This is a severe limitation to the development of an IBI, which depends on the comparison of least- to most-disturbed wetlands (Karr and Chu 1999, Teels and Adamus 2002). Because of this, the U.S. EPA has recommended using targeted sampling to develop IBIs (Danielson 2002, Teels and Adamus 2002). Indeed, an examination of site data collected in the first field season of this project revealed that reference condition wetlands and, in the case of depressional wetlands, highly disturbed wetlands, had not been adequately sampled. Additional wetlands were therefore inventoried as described under Targeted Sampling below.

Two wetland classes, depressional and riverine, were sampled. The depressional class was restricted to temporarily and seasonally flooded wetlands as defined by Cowardin et al. (1979) and mapped by the National Wetland Inventory (NWI). Temporarily and seasonally flooded wetlands make up the vast majority of prairie potholes in the study area. According to NWI coverage in the Middle Milk sub-basin (Figure 2), 68% of potholes are classified as temporarily flooded, 30% as seasonally flooded, and 2% as semipermanently flooded. Riverine sampling locations were chosen from Milk River tributaries that ranged from 0–2% valley slope. Initial criteria for site selection are presented in the following section.

Watershed Ranking

Wetlands were initially sampled using a stratified random design. The 4^{th}-level Middle Milk sub-basin is comprised of 24 5^{th}-level watersheds. These watersheds were ranked based on 12 factors that represent landscape-scale surrogates of human disturbance (Table 1). Factor values were calculated for each watershed using a geographical information system (GIS; ArcView 3.2, ESRI, Redlands, California 92373). To minimize scaling issues among factors, factor values were rounded to the nearest integer, and watersheds were ranked based on those rounded values with ties receiving the same rank. For example, three watersheds with road densities of 1.98, 2.29, and 3.15 (rounded values of 2, 2, and 3) would be ranked 1, 1, and 2, respectively. Watersheds were ranked based on ascending values, except for percent federal land, wilderness, and land cover, which were ranked by decreasing values. Sample watersheds were then selected based on their overall mean rank.

To evaluate the land cover category, each cover class was assigned a weight between 0 and 1 (Table 2). This weighting scheme, based on Hauer et al. (2002a, b), represents the degree to which land cover types affect wetland functionality. Land cover types weighted 1 are natural habitats that provide the same functional value as reference conditions. Decreasing weights indicate an increasing departure from reference conditions and a resulting loss of functional value. Land cover scores were calculated by multiplying the percent of the watershed in each land cover type by that type's functional weight and then summing and multiplying by 100. Thus a watershed with only natural vegetation would score 100, while lower scores represent conversions to human land uses.

Assuming that the condition of a watershed's population of wetlands was correlated with watershed rank, the three least impacted (highest ranked) watersheds, three most impacted (lowest ranked) watersheds, and three moderately impacted (middle ranked) watersheds were selected. Because some of the initially selected watersheds occurred primarily on Tribal land, where access was limited, alternatives (next ranked watersheds) were selected. Selected watersheds are shown in Figure 3.

Individual sampling points were then randomly chosen within each selected watershed. Twenty-seven wetlands were sampled from each class (three depressional and three riverine wetlands sampled in each of the nine watersheds). If a wetland could not be sampled because access to private land was not granted, another wetland was randomly selected.

Depressional wetlands were selected using NWI coverage. The sample population was considered to be all wetlands classified as temporarily or seasonally flooded palustrine emergent (PEMA and PEMC, Cowardin et al. 1979). The riverine sample

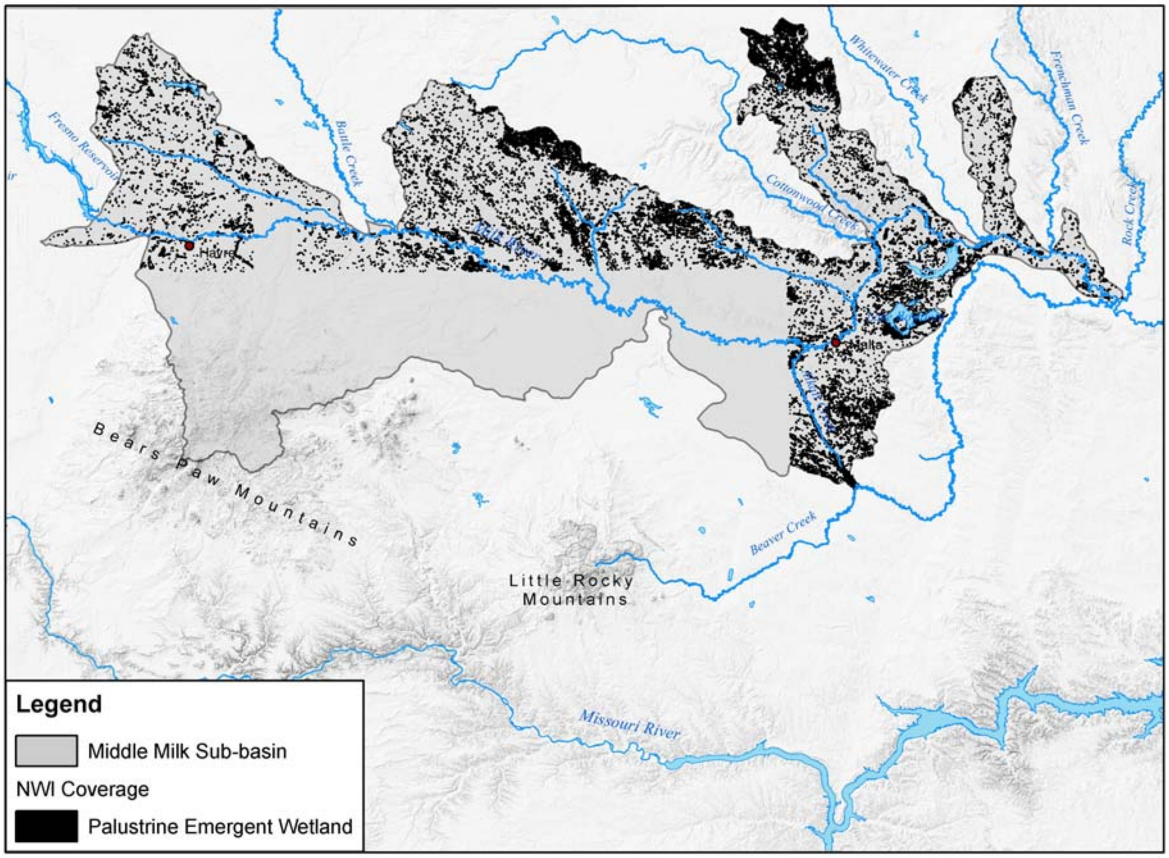

Figure 2. Extent of national wetland inventory coverage in the study area.

population was defined as stream reaches of Milk River tributaries that had a valley gradient from 0.0001–2.0% and a minimum length of 100 m. Reaches were identified by combining the 2001 National Elevation Dataset (30-m digital elevation model) with the 1999 1:100,000 National Hydrography Dataset. Reaches were then broken into 1 km segments (minimum segment length of 100 m) with the 100-m reach at the segment midpoint being the sample unit.

Targeted Sampling

Fifty-six sites were sampled in 2002: 27 depressional and 29 riverine wetlands (27 randomly chosen and two targeted samples that appeared to represent reference conditions). During the course of this field work, it appeared that the probabilistic sampling strategy was not representing the full range of wetland condition. Primarily, reference condition wetlands were not being adequately sampled. Therefore, additional wetlands were targeted in 2003. Reference wetlands were identified in consultation with federal and state resource agency personnel and local experts in Montana and Saskatchewan. Based on this consultation, an additional 11 wetlands were sampled in 2003. These consisted of six depressional wetlands, four in reference condition and two highly disturbed, and five reference condition riverine wetlands.

DATA COLLECTION

Sample wetlands were stratified by hydrological and geomorphological parame-

Table 1. Human disturbance factors used to rank 5th-level watersheds in the Middle Milk sub-basin.

Human Disturbance Factor	Unit of Measurement
Water Rights Irrigation	Percent
Population Density	Persons per Square Mile
Corps 404 Stream/Wetland Permits	Permits per 100 Square Miles
S303d Listed Streams	Meters per Square Mile
Road Density	Miles per Square Mile
Well Density	Wells per Square Mile
Mine Density	Mines per Square Mile
Discharge Permit Density	Permits per Square Mile
Road/Stream Crossings	Crossings per 10 Square Miles
Federal Land	Percent
Wilderness	Percent
Land Cover	Percent

ters. Depressional wetlands were stratified by inundation period using the zones described by Stewart and Kantrud (1971) (i.e., wet meadow and shallow marsh, corresponding to temporarily and seasonally flooded, respectively). Riverine wetlands were stratified by geomorphology (i.e., depositional bar, channel shelf, floodplain (*sensu* Hupp and Osterkamp 1985)). Vegetation was sampled from each fluvial surface or inundation zone and was characterized using randomly placed 1.0-m × 0.5-m quadrats. Abundance of each vascular plant species was estimated as percent canopy cover within quadrats. Random quadrat samples were repeated until no new species were found and then one more quadrat was sampled. For multimetric and multivariate

Table 2. Functional weights assigned to land cover types.

Land Cover	Functional Weight
Forest	1.0
Grassland	1.0
Shrubland	1.0
Snow	1.0
Water	1.0
Wetland	1.0
Pasture	0.6
Barren	0.5
Orchards	0.5
Residential (low)	0.4
Crops	0.2
Mines/Quarries	0.2
Residential (high)	0.2
Commerce/Industrial	0.1

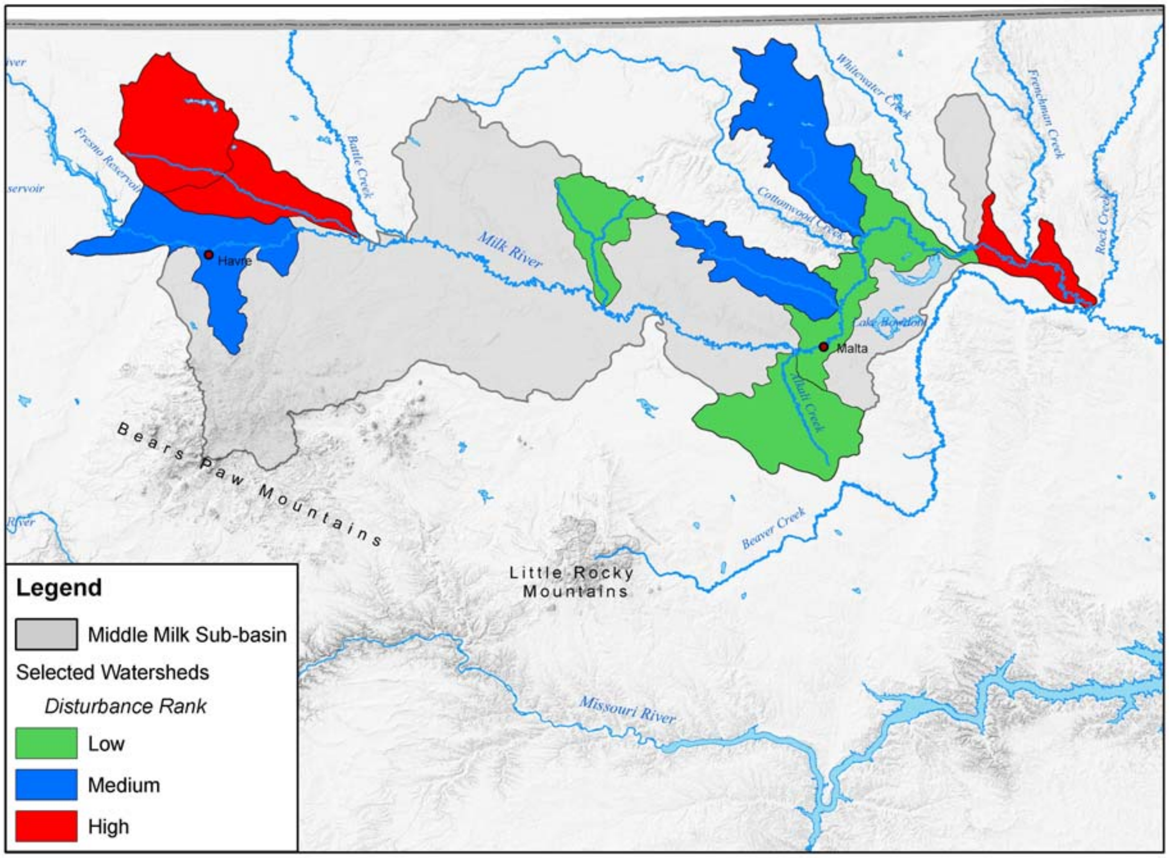

Figure 3. Selected 5th-level watersheds and their relative disturbance categories.

analyses, quadrat data were aggregated by zone/fluvial surface and site. Nomenclature follows Kartesz (1999), which forms the basis for the national naming standard for vascular plants (U.S. Department of Agriculture 2004).

Environmental factors recorded at each site included hydrologic and geomorphic modifications (e.g., presence and extent of ditches, dikes, tiles, revetment, slumped or unstable banks), physical site disturbances (e.g., presence and extent of pugging and hummocking), and land use within the wetland and adjacent uplands.

DATA ANALYSIS

Human Disturbance Parameters

Watershed disturbance categories, based on ranking 5th-level hydrologic unit watersheds, were initially used to sample wetlands across a putative human disturbance gradient. However, the correspondence between watershed ranks and human disturbance at a particular site was unknown. To test what relationship, if any, watershed ranks had to site condition, additional human disturbance parameters were measured for each site. These parameters spanned multiple spatial scales: within the wetland or sample reach, within a 500-m buffer around the site, and within the site's upstream catchment (riverine wetlands only). The buffer width of 500 m was chosen in part because it included an area sufficient to encompass the catchments of most depressional wetlands.

At the local scale (within the depressional wetland or riverine sample reach), grazing intensity and previous agricultural use were considered. Grazing intensity was defined as low, medium, or high (low/medium and high for depressional wetlands) based on bank stability and the extent of ground disturbance, such as pugging or hummocking. Previous agricultural use was binary (none, site previously tilled; depressional wetlands only). Human disturbance at the buffer and catchment scale were characterized using a GIS (ArcGIS 8.3, ESRI, Redlands, California 92373). Catchments upstream from riverine sample locations were delimited using the hydrology modeling extension in ArcGIS 8.3. This routine uses a sink-filled digital elevation model (DEM) to define catchments. The base DEM used was from the 30-m raster National Elevation Dataset. The extent of landscape-scale human disturbance within buffers and catchments was characterized by measuring land cover, road density, and the number of dams (catchment-scale only).

Land cover was determined from the National Land Cover Database (30-m raster data). Land cover types (e.g., grassland/herbaceous, shrubland, row crop, fallow, pasture/hay) were grouped into two classes, native vegetation and agricultural, and the proportion of the buffer or catchment in each class was measured. Other human-modified land covers, such as developed areas, did not occur within buffers or catchments examined. Buffer and catchment road density was calculated from 2000 U.S. Census Bureau TIGER 1:100,000 line files. The number of dams in a catchment was determined from the Montana Dams Database (a compilation of the U.S. Army Corps of Engineers National Inventory of Dams and the U.S. Geological Survey Geographic Names Information System that is maintained by the Montana Department of Fish, Wildlife & Parks).

As an alternative to watershed disturbance categories, I used a rule-based disturbance hierarchy to construct numerical disturbance indices for depressional and riverine wetlands, similar to Lopez and Fennessy (2002). These indices integrated disturbance factors across spatial scales. The relative importance of landscape vs. site-level disturbance factors to the biological community varies by system and taxa (Bisson et al. 2002, Seabloom and van der Valk 2003, Wright et al. 2003). Based on previous research and personal observation, I assumed that vegetation was responding primarily to on-site disturbances. Therefore, for depressional wetlands, the disturbance hierarchy included on-site agricultural disturbance, on-site grazing disturbance, and road density within a 500-m buffer (Figure 4). These factors have all been shown to influence wetland vegetation, faunal assemblages, and functionality of prairie potholes (Kantrud et al. 1989, Euliss and Mushet 1996, Kantrud and Newton 1996, Euliss and Mushet 1999, Freeland and Richardson 1999, Euliss et al. 2001) or wetlands generally (Findlay and Houlahan 1997, Trombulak and Frissell 2000, Houlahan and Findlay 2003). The disturbance hierarchy for riverine wetlands used on-site grazing intensity and hydrological modification, as measured by the number of dams in the upstream catchment (Figure 5). Both these factors can greatly influence riparian vegetation and wetland function (Kauffman and Krueger 1984, Schulz and Leininger 1990, Boggs and Weaver 1994, Scott et al. 1997, Auble and Scott 1998, Friedman et al. 1998, Scott et al. 2003).

Table 3 lists the disturbance factors used and how each factor was scored. Grazing intensity and agricultural use were categorical variables. To place values for road density or number of dams into disturbance categories, quantile plots were examined for these variables. Break points for disturbance categories were determined by trisecting the value range of each variable.

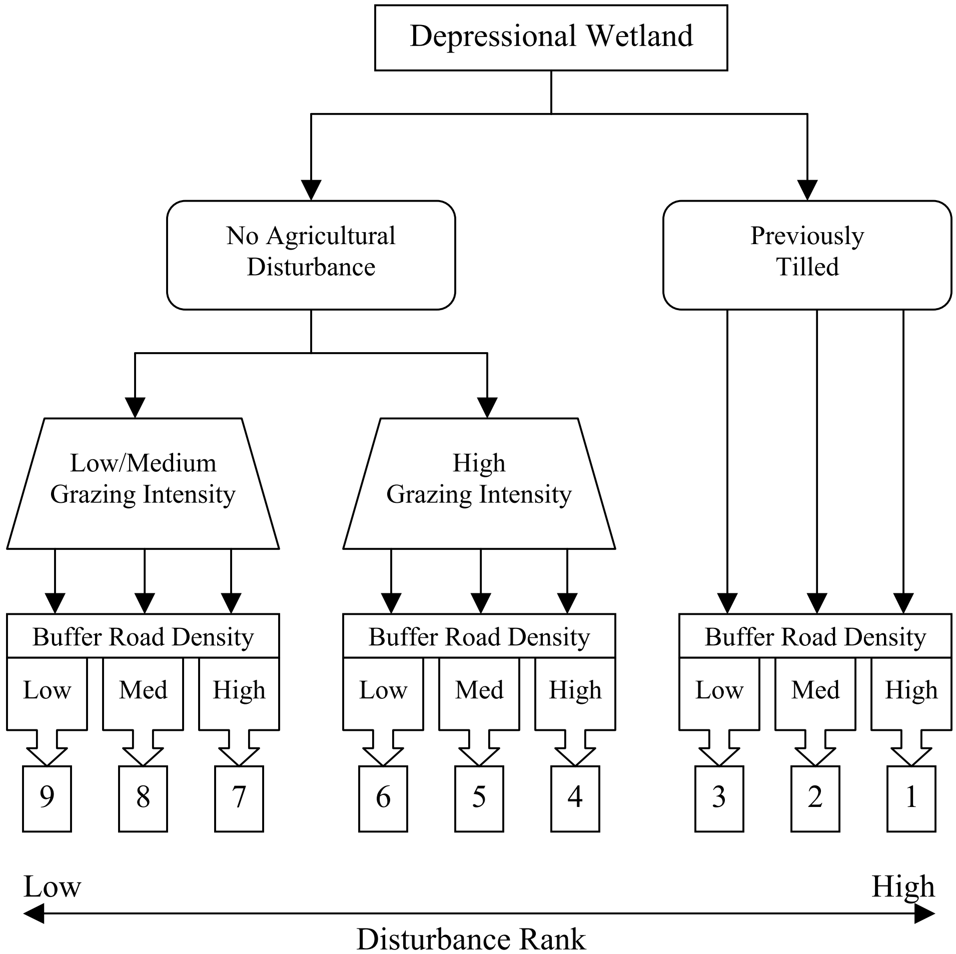

Figure 4. Schematic illustrating how temporarily and seasonally flooded depressional wetlands were ranked along a human disturbance gradient.

Relationships between watershed disturbance categories and other disturbance measures were analyzed using Kruskal-Wallace tests (SYSTAT 2002). The Kruskal-Wallace procedure is a non-parametric analog to one-way analysis of variance and was used because data did not meet assumptions of homogeneity of variance (Levene 1960). In addition, I examined the relationship between disturbance categories and vegetation response variables selected as metrics (see Multimetric Methods below), also using Kruskal-Wallace tests.

Multimetric Methods

Multimetric analysis seeks to determine the health of a site, such as a waterbody or wetland, by directly measuring the condition of one or more components of its biota, such as vegetation or macroinvertebrates (Danielson 2002). This method is based on defining a relatively homogeneous study environment (e.g., high- or low-gradient streams, depressional wetlands) and measuring the response of target biota across a gradient of human disturbance (Karr and Chu 1999). The response is calculated by assessing measurable attributes of the biological system. Attributes that increase or

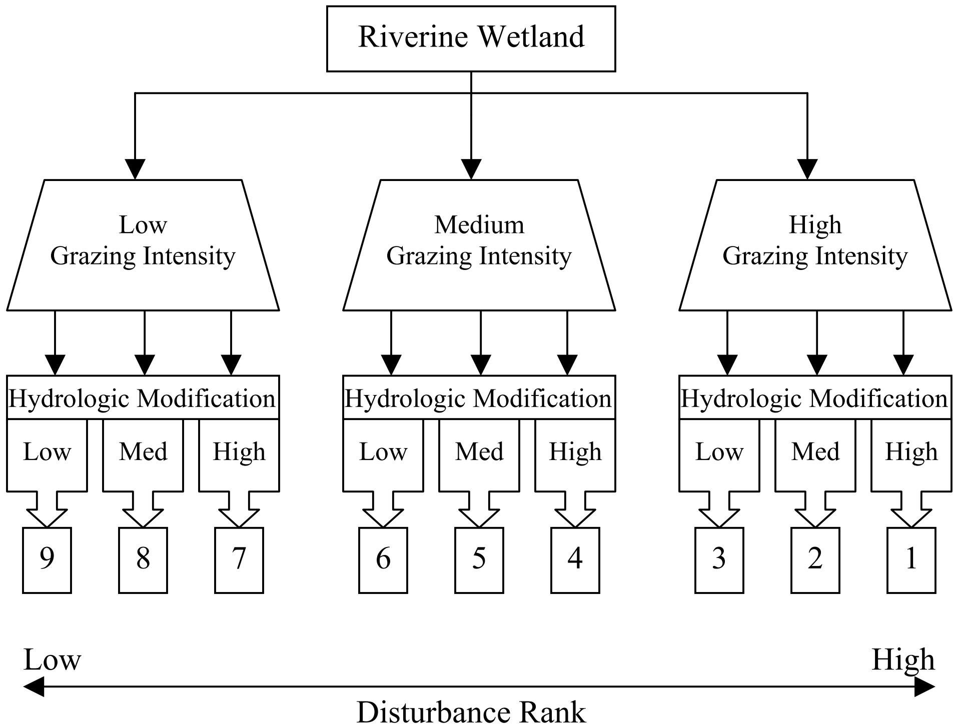

Figure 5. Schematic illustrating how herbaceous-dominated intermittent and ephemeral riverine wetlands were ranked along a human disturbance gradient.

decrease predictably with increasing human disturbance, are sensitive to a range of biological stresses, discriminate between human-caused perturbations and natural variability, and are easy to measure and interpret can be successfully used as metrics (Karr and Chu 1999). Multimetric approaches, such as indices of biological integrity, combine metrics reflecting diverse biotic responses to anthropogenic stressors into an integrative measure of biological condition (Karr and Chu 1999, Teels and Adamus 2002).

Attributes can be divided into several categories: species richness and composition, tolerance/intolerance to human disturbances, trophic composition, and population characteristics (Teels and Adamus 2002). In regards to vegetation, these attribute categories can be refined to those representing community-based metrics, metrics based on plant functional groups, and species-specific metrics (Fennessy et al. 2002). Examples of metrics include changes in species richness and dominance (community-based metrics), changes in the number of perennials, annuals, or intolerant species (plant functional group metrics), and dominance of individual species (species-specific metrics).

In this study, two wetland classes were sampled, temporarily and seasonally flooded depressional wetlands and intermittent and ephemeral riverine wetlands, and human disturbance was measured along numerical disturbance indices. Thirty-five vegetation attributes were examined. Many of these attributes were chosen because they had been proven to be successful vegetation metrics for wetlands in western Montana (Borth 1998), North Dakota (DeKeyser et al.

Table 3. Disturbance factors used to develop human disturbance indices for depressional and riverine wetlands.

Disturbance Factor	Scale	Wetland Type	Criteria
Agricultural Use	Local	Depressional	Low: No evidence that wetland was previously tilled High: Evidence of past tillage, such as plow lines or rock piles
Grazing Intensity	Local	Depressional/ Riverine	Low: Banks stable with little or no slumping, little to no pugging or hummocking Med: Moderate or localized bank erosion or slumping, some pugging or hummocking present High: Extensive bank erosion or slumping over channel length, extensive pugging or hummocking
Road Density	Buffer	Depressional	Low: < 5 m/ha Med: 5–63 m/ha High: > 63 m/ha
Hydrological Modification	Catchment	Riverine	Low: 0 dams/1,000 ha Med: 0.01–0.3 dams/1,000 ha High: > 0.3 dams/1,000 ha

2003), Ohio (Mack et al. 2000, Mack 2001), or Minnesota (Helgen and Gernes 2001). Potential metrics and their predicted response to human disturbance are listed in Table 4. The relationship between attributes and site disturbance index was examined graphically and with Spearman rank-order correlation coefficients (r_s). Metrics showing a strong linear or curvilinear response to disturbance and that differentiated between least and most disturbed wetlands were chosen for inclusion into the multimetric index. Where two or more metrics that conveyed a similar biological response had a robust response to disturbance (e.g., Shannon and Simpson diversity indices), the metric with the higher r_s value or greater ecological relevance was chosen.

To combine individual metrics into a multimetric index, metric data was converted into a common scoring base. The scoring base used was that recommended by Karr and Chu (1999), where metric values that represent reference conditions are scored 5, those that deviate somewhat from reference condition are scored 3, and those that strongly deviate from reference condition are scored 1. For metrics with a linear response to disturbance, quantile plots were used to determine value ranges for scoring categories. Break points were calculated for the 67th and 33rd quantiles, except where modified due to natural breaks in values or ties. Value ranges for metrics with a curvilinear response were determined by graphical fitting. Total multimetric scores were calculated by summing metric scores and dividing by the number of metrics. Thus the multimetric index developed for each wetland class would have common values, even if the number of individual metrics differed.

Table 4. Vegetation attributes initially considered as potential metrics for depressional and riverine wetlands and their predicted response to increasing human disturbance. dep = depressional wetlands, riv = riverine wetlands

Vegetation Attribute	Predicted Response
Richness of native genera	decrease
Shannon diversity index (H)	increase (dep)/ decrease (riv)
Simpson's diversity index (D)	increase (dep)/ decrease (riv)
Total species richness	decrease
Richness of native perennials	decrease
Richness of native graminoids	decrease
Richness of intolerant graminoids (C-value ≥ 6)	decrease
Richness of *Carices*	decrease
Richness of dicots	increase (dep)/ decrease (riv)
Richness of annual or biennial species	increase
Richness of exotic species	increase
Richness of species with C-value ≥ 4	decrease
Richness of species with C-value ≥ 5	decrease
Richness of intolerant species (C-value ≥ 6)	decrease
Richness of tolerant species (C-value ≤ 2)	increase
Richness of species with a wetland indicator status of FAC or wetter	decrease
Richness of hydrophytes (wetland indicator status of FACW or wetter)	decrease
Proportion of total species richness comprised of annual or biennial species	increase
Proportion of total species richness comprised of exotic species	increase
Proportion of total species richness comprised of tolerant species (C-value ≤ 2)	increase
Relative cover of native perennials	decrease
Relative cover of native graminoids	decrease
Relative cover of intolerant graminoids (C-value ≥ 6)	decrease
Relative cover of *Carices*	decrease
Relative cover of dicots	increase (dep)/ decrease (riv)
Relative cover of annual or biennial species	increase
Relative cover of exotic species	increase
Relative cover of species with C-value ≥ 4	decrease
Relative cover of species with C-value ≥ 5	decrease
Relative cover of intolerant species (C-value ≥ 6)	decrease
Relative cover of tolerant species (C-value ≤ 2)	increase
Relative cover of species with a wetland indicator status of FAC or wetter	decrease
Relative cover of hydrophytes (wetland indicator status of FACW or wetter)	decrease
Floristic quality index	decrease
Average C-value	decrease

How well multimetric indices reflected site condition (as measured by the disturbance index) was assessed using linear regression. Assumptions of linear regression were tested by examining normal probability plots of residuals (assumption that errors are normally distributed) and scatter plots of studentized residuals against estimated values (assumptions that errors have constant variance and are independent) (SYSTAT 2002). Goodness-of-fit of multimetric indices was also assessed using the multivariate methods described in the following section.

<u>Floristic Quality Index</u>

One of the vegetation attributes considered as a metric was the floristic quality index (FQI). Floristic quality assessments were initially developed by Swink and Wilhelm (1979) for plant communities in the Chicago area. This method has since been expanded for use in other areas of the Midwest. Its usefulness as a vegetation metric has been demonstrated by DeKeyser (2000) and Mushet et al. (2002) for prairie potholes in North Dakota and by Lopez and Fennessy (2002) for wetlands in Ohio. (However, see Matthews (2003) concerning problems of comparing FQI scores across wetland types.) This method assigns a coefficient of conservatism (C) to all native species that occur in a specified region. This coefficient, which ranges from 0 to 10, represents a species' relative tolerance to disturbance. The interpretation of coefficient values is as follows (from Fennessy et al. 1998):

Value	Interpretation
0	alien taxa and those natives that are opportunistic invaders or common components of ruderal communities;
1-3	widespread taxa that are found in a variety of communities, including disturbed sites;
4-6	taxa that display fidelity to a particular community, but tolerate moderate disturbance to that community;
7-8	taxa that are typical of well established communities which have sustained only minor disturbance;
9-10	taxa that exhibit high degrees of fidelity to a narrow set of ecological conditions.

In this study, I used C values established for native species in the Dakotas (Northern Great Plains Floristic Quality Assessment Panel 2001). The floristic quality index is calculated as

$$FQI = \Sigma C / \sqrt{n}$$

where FQI = floristic quality index, C = coefficient of conservatism, and n = richness of native species.

In addition to the FQI itself, several other vegetation attributes based on C-values, such as richness and relative cover of species with certain C values and the average C-value of a sample unit, were calculated (Table 4).

<u>Diversity Measures</u>

Two diversity measures were considered, the Shannon and Simpson diversity indices. Both of these indices are related to and based partially on species richness. However, these measures also incorporate the equitability of species' abundance as well. For example, for both indices a plot containing three species where one species is dominant would be rated as being less diverse than a three-species plot where the species occurred with equal abundance.

The Shannon diversity index is calculated as

$$H' = -\Sigma p_i \log p_i$$

where H' = Shannon diversity index and p_i = the relative cover of the i^{th} species within a sample unit.

The Simpson diversity index is calculated as

$$D = 1 - \Sigma p_i^2$$

where D = Simpson diversity index and p_i = the relative cover of the i^{th} species within a sample unit.

These two measures are similar but vary in their sensitivity to rare species: Shannon diversity is intermediate between species richness and Simpson diversity in its sensitivity to rare species.

Multivariate Methods

Multivariate analyses were performed to validate the multimetric approach and to assess the response of the entire vegetation community to human disturbance. These analyses included parametric and non-parametric comparisons of group differences and indirect ordination. First, group differences were assessed by assigning sites to disturbance categories. These categories were created by combining sites into groups representing reference condition wetlands (disturbance index scores of 7–9), moderately disturbed wetlands (disturbance index scores of 4–6), and severely disturbed wetlands (disturbance index scores of 1–3). The ability of metrics to correctly classify sites into these three groups was assessed using discriminant analysis. Discriminant analysis is an eigenanalysis technique that finds linear functions that best separate cases into predefined groups and was used to predict group membership based on metric values. Predicted and actual group memberships were compared to determine how well metrics discriminated among disturbance categories. Linear discriminant analysis was performed using the complete estimation method (SYSTAT 2002). Assumptions of multivariate normality and homogeneity of within-group variance were not met in all cases; however, this was not considered critical as the analysis was exploratory (McCune and Grace 2002).

Multi-response permutation procedure (MRPP, Biondini et al. 1988) was used to test whether plant community composition for all species sampled at a site differed among disturbance categories (PC-ORD, McCune and Mefford 1999). In addition to a P-value, MRPP describes group tightness with A, a statistic that compares the within-group heterogeneity to that expected by chance (A = 1 when items are identical within groups, A = 0 when heterogeneity within groups equals that expected by chance, and A < 0 when heterogeneity within groups is greater than that expected by chance) (McCune and Mefford 1999). To improve the correspondence of MRPP results with non-metric multidimensional scaling (see below), MRPP was based on a rank-transformed Sørensen distance matrix (McCune and Grace 2002). Where community composition differed significantly with disturbance, associations between species and groups was examined using indicator species analysis (Dufrêne and Legendre 1997). This method assigns each species an indicator value for a particular group that ranges from 0 (no indication) to 100 (perfect indication). The statistical significance of indicator values was tested using a Monte Carlo randomization procedure with 10,000 iterations.

To examine relationships among species and between species and environmental factors, sample sites were ordinated in species space using non-metric multidimensional scaling (NMS, Kruskal 1964, Mather 1976). Ordination is a data reduction method that attempts to describe underlying patterns of species composition by graphically summarizing complex relationships (McCune and Grace 2002). NMS is an indirect ordination technique that works without assuming that a species responds to environmental gradients in a linear or unimodal fashion and is robust to large numbers of zero values. It therefore avoids many of the distortions of eigenvector-based ordination methods, such as detrended correspondence analysis (Kenkel and Orlóci 1986, Minchin 1987). NMS is an iterative method that attempts to reduce differences between the ranked distances in the original multidimensional species space and ranked distances in the reduced dimensions of the ordination. These differences, termed stress, are measured as the degree of departure from monotonicity in the original space and the reduced space (McCune and Grace 2002). Dimensionality was determined by running NMS on PC-ORD's autopilot mode for 40 runs with real data and 50 runs with randomized data in each of six dimensions (McCune and Mefford 1999). Dimensionality was chosen by selecting the highest number of dimensions that appreciably reduced stress and where the final stress for real data was significantly lower than that for randomized data. Additional parameters included the use of the quantitative version of the Sørensen distance measure, the global form of NMS, and an instability criterion of 0.00001 to be achieved after 500 iterations or 50 continuous iterations within the criterion. To reduce beta diversity (β_w, compositional heterogeneity among sample units (Whittaker 1972)) and improve the interpretability of results, species occurring in fewer that 5% of sample units were omitted from the analysis.

RESULTS

WATERSHED DISTURBANCE CATEGORIES

Watershed disturbance categories showed no statistically significant relationship with other measures of human disturbance (Kruskal-Wallace tests, $\alpha = 0.05$). This lack of correspondence was observed for both depressional and riverine datasets and held true for disturbance factors measured within a 500-m buffer around sites and within the upstream catchment (riverine sites only) as well as for an integrative site disturbance index (Figures 6 and 7). Vegetation metrics were also compared among watershed disturbance categories (Kruskal-Wallace tests, $\alpha = 0.05$). These comparisons also showed no statistical relationship, except for two metrics for depressional wetlands, the relative cover of native perennials and the relative cover of exotic species (Figures 8 and 9). Both these metrics strongly respond to whether or not a site has been previously tilled, and the significant results are the product of the clustering of agriculturally disturbed sites within one watershed ranked at medium disturbance.

DEPRESSIONAL WETLANDS

Metrics and the Multimetric Index

Seven of the 35 attributes examined showed a robust response to the human disturbance gradient (Figure 10). The response of two of these attributes, the Shannon and Simpson diversity indices, was observed within the shallow marsh zone of seasonally flooded wetlands only. One of the precepts of the multimetric method is that individual metrics will represent different aspects of the biological response to human disturbance. Therefore, biologically redundant metrics should be avoided (Kimberling et al. 2001, Karr and Kimberling 2003). Of the seven potential metrics, two pairs of attributes were biologically redundant. These were the relative cover of native perennials and relative cover of native graminoids and the Shannon and Simpson diversity indices. Sixty-two percent of native perennials were also native graminoids and the two values for the two metrics were highly correlated

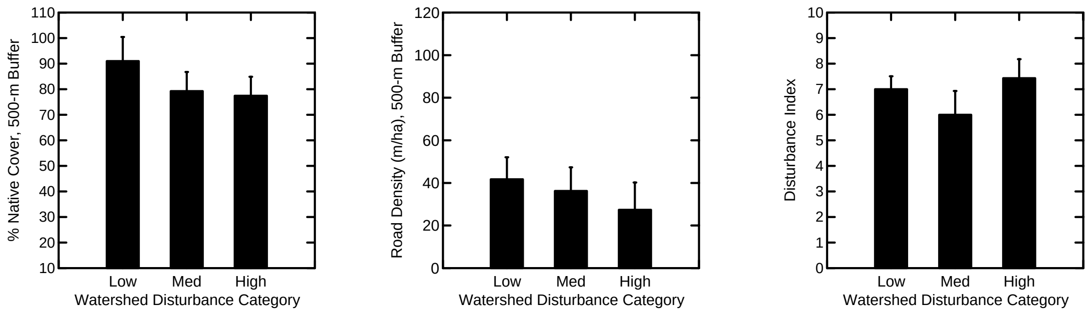

Figure 6. Bar graphs of disturbance measures by watershed disturbance categories for temporarily and seasonally flooded depressional wetlands. Bars are mean values ± 1 SE. Comparisons among disturbance categories were non-significant for all factors (Kruskal-Wallace tests).

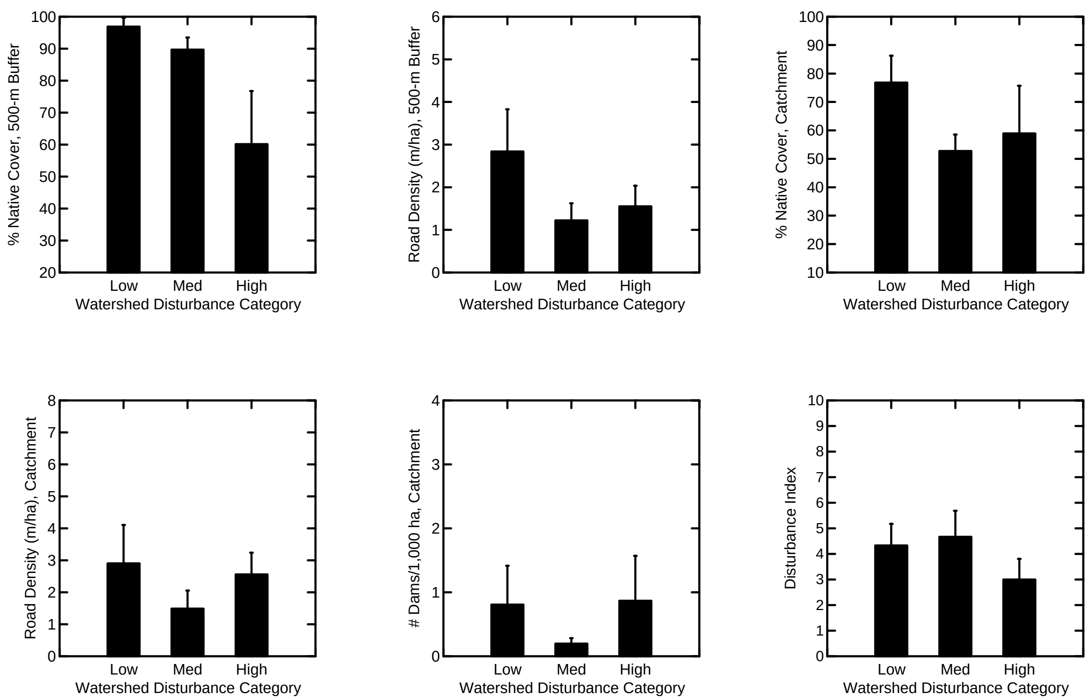

Figure 7. Bar graphs of disturbance measures by watershed disturbance categories for herbaceous-dominated intermittent and ephemeral riverine wetlands. Bars are mean values ± 1 SE. Comparisons among disturbance categories were non-significant for all factors (Kruskal-Wallace tests).

(r_s = 0.899); similarly, Shannon and Simpson diversity were highly correlated (r_s = 0.944). The relative cover of native perennials was selected over the relative cover of native graminoids because it was inclusive of more species (34 vs. 23) and had a stronger correlation to the disturbance index (r_s = 0.747 vs. r_s = 0.709). Although the correlation between Shannon diversity and site disturbance was greater than that for Simp-

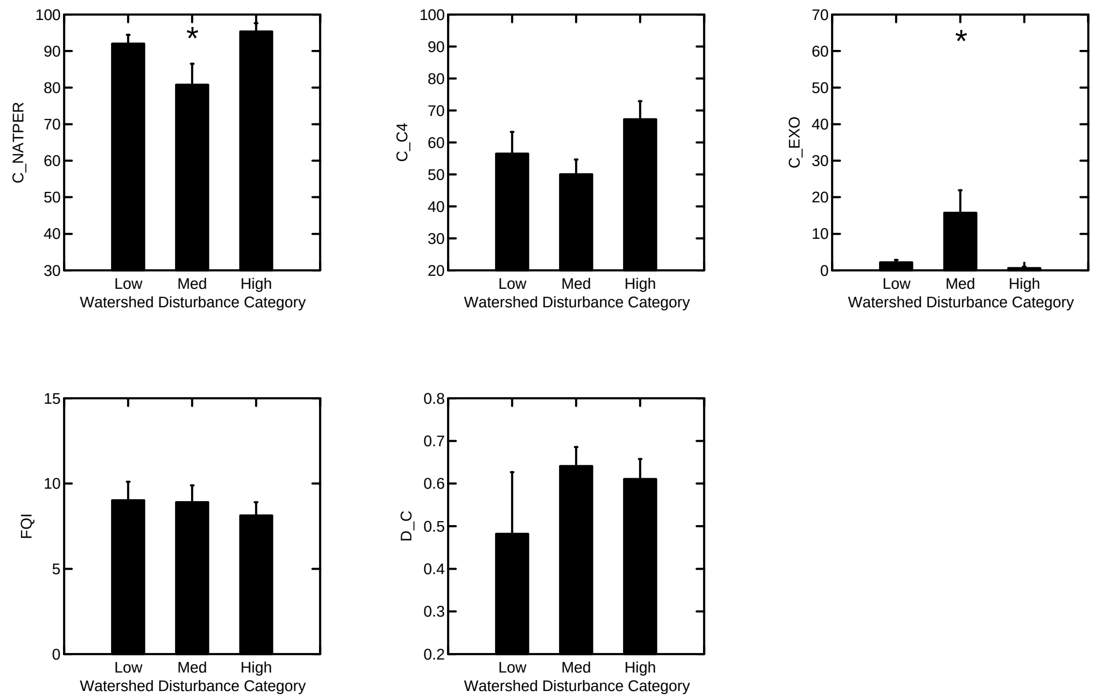

Figure 8. Bar graphs of vegetation metrics by watershed disturbance categories for temporarily and seasonally flooded depressional wetlands. Bars are mean values ± 1 SE. Graphs with asterisks indicate that the metric was significantly different among disturbance categories (Kruskal-Wallace tests, $P \leq 0.05$).

son diversity ($r_s = -0.598$ vs. $r_s = -0.469$), Simpson diversity was chosen because its intrinsic properties made it a more robust measure when comparing sites/inundation zones that had been sampled with varying intensity. The vegetation sampling protocol did not specify a uniform number of quadrats per site or per area. The Simpson diversity index ameliorates problems associated with uneven sampling intensity because it is little affected by rare species and is therefore relatively stable with sample size (McCune and Grace 2002).

Value ranges for selected metrics were calculated based on quantile plots for attributes with a linear response (relative cover of species with C value ≥ 4, floristic quality index, and Simpson diversity index) and by graphical fitting for attributes with a curvilinear response (relative cover of native perennials and relative cover of exotic species). Value breaks for quantile plots were determined at the 33rd and 67th quantiles, with some variability based on natural breaks in the data or tied values. Value ranges are presented in Table 5. The resulting multimetric index showed a significant response to human disturbance, as measured by the site disturbance index ($F_{1, 28} = 47.505$, $R^2 = 0.629$, $P < 0.001$, Simpson diversity metric not included; Figure 11).

The Simpson diversity metric was only observed to be valid within the seasonally flooded zone, which is naturally less diverse than the adjoining temporarily flooded zone (personal observation). As the goal of this study was to produce metrics that are valid for both temporarily and seasonally flooded depressional wetlands, I tested whether the Simpson diversity metric

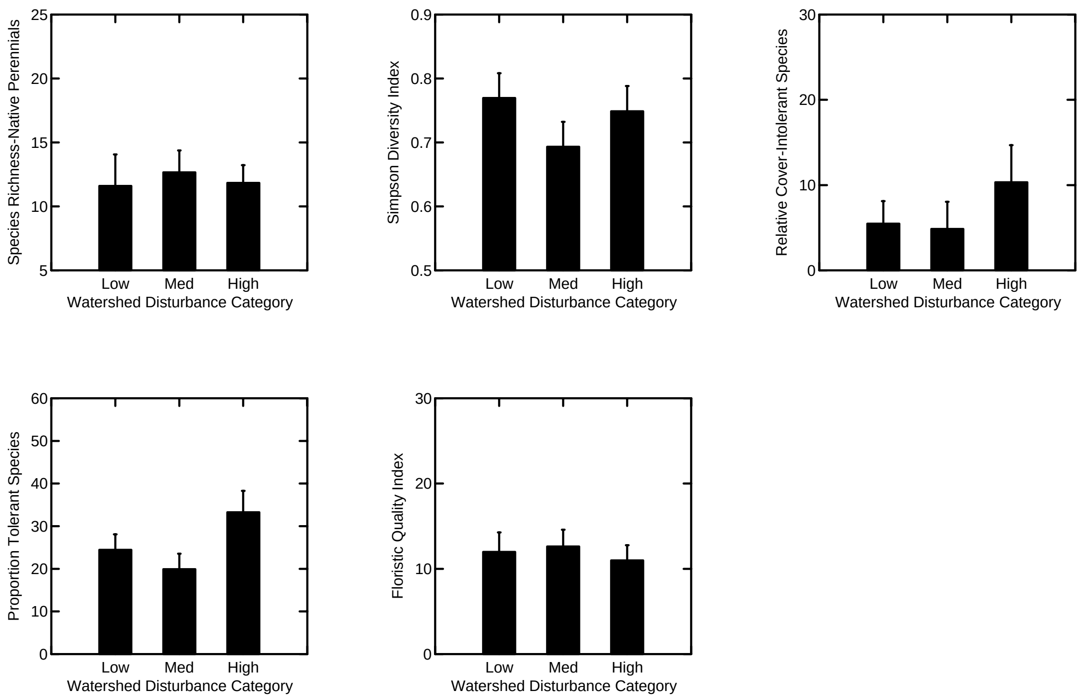

Figure 9. Bar graphs of vegetation metrics by watershed disturbance categories for herbaceous-dominated intermittent and ephemeral riverine wetlands. Bars are mean values ± 1 SE. Comparisons among disturbance categories were non-significant for all factors (Kruskal-Wallace tests).

added appreciably to the multimetric index by comparing linear regressions of the multimetric index with and without the diversity metric for the 18 seasonally flooded depressional wetlands sampled. The linear regression without the diversity metric produced higher F and R^2 statistics (with D: $F_{1, 16} = 49.755$, $R^2 = 0.757$, $P < 0.001$, without D: $F_{1, 16} = 57.129$, $R^2 = 0.781$, $P < 0.001$). The Simpson diversity index was therefore dropped as a metric.

When sites were divided into disturbance categories (reference condition, moderately disturbed, and severely disturbed), vegetation metrics correctly classified a site's disturbance category membership for 5 out of 5 severely disturbed sites, 5 out of 7 moderately disturbed sites, and 12 out of 18 reference condition sites for an overall classification accuracy of 73% (results based on discriminant analysis; Figure 12).

Vegetation Community Response

In addition to the selected metrics, the whole vegetation community in sampled depressional wetlands also responded to human disturbance. Plant community composition and abundance was significantly different among disturbance categories (severely disturbed, moderately disturbed, and reference condition) (MRPP, A = 0.189, P < 0.001). This is a fairly robust finding, as A-values in community ecology are commonly less than 0.1, even when the test is significant (McCune and Grace 2002). Vegetation differences among disturbance categories are graphically displayed in the results from the NMS ordination (three-dimensional solution, final stress = 8.197, instability =

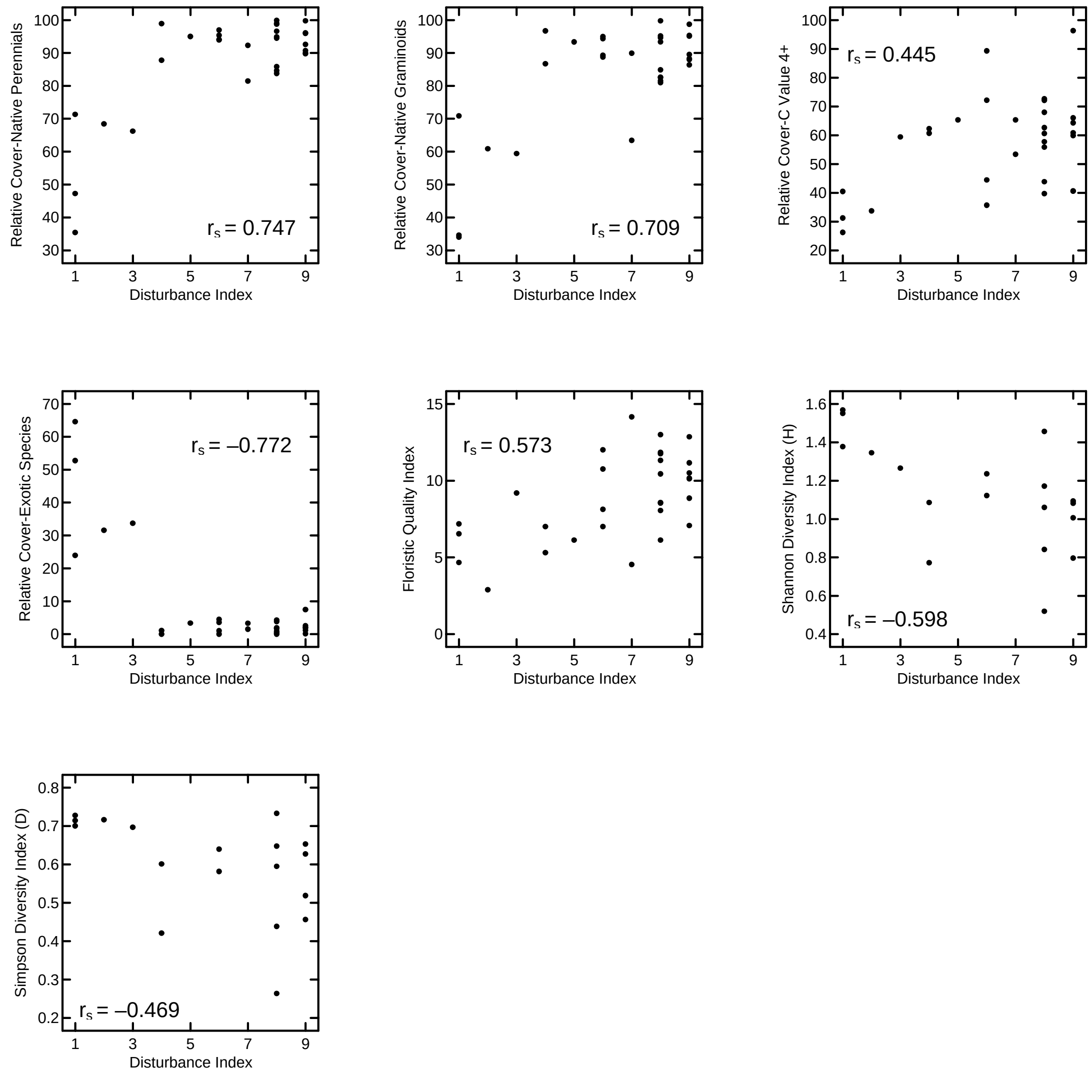

Figure 10. Scatter plots of attribute values against site disturbance index for temporarily and seasonally flooded depressional wetlands. Shown are vegetation attributes that had a linear or curvilinear response to human disturbance and differentiated between least and most disturbed sites. Disturbance index ranges from 1 (most disturbed) to 9 (least disturbed). r_s = Spearman rank-order correlation coefficient. Data for Shannon and Simpson diversity indices are for the shallow marsh zone of seasonally flooded wetlands only.

0.00001, 72 iterations; Figure 13). Species that were significantly associated with severely disturbed and reference condition wetlands are presented in Table 6 (indicator species analysis; no species were significantly associated with moderately disturbed wetlands).

RIVERINE WETLANDS

In contrast to depressional wetlands, riverine wetlands are naturally highly variable. This is especially true of small-order ephemeral streams in arid and semi-arid environments (Friedman and Lee 2002, Eby et

Table 5. Ranges of attribute values for metric scoring categories for temporarily and seasonally flooded depressional wetlands. Relative cover values are expressed as percentages.

Metric	Value Range for 1	Value Range for 3	Value Range for 5
Relative cover of native perennials	< 75	75–90	> 90
Relative cover of species with C-value ≥ 4	< 40	40–64	> 64
Relative cover of exotic species	> 10	10–5	< 5
Floristic quality index	< 6.7	6.7–10.1	> 10.1
Simpson diversity index*	> 0.68	0.68–0.55	< 0.55

* metric is for seasonally flooded wetlands only

al. 2003). Thirty-four riverine wetlands were sampled in the course of this study. These sites encompassed a wide range of environmental heterogeneity, including perennial and ephemeral streams, alkaline and non-alkaline systems, and vegetation dominated by herbaceous and woody species. When these sites were considered together, the "noise" of this natural variability made it difficult to detect the "signal" from anthropogenic stressors. To restore a workable level of environmental homogeneity, sites that sampled alkaline or perennial streams were removed from the analysis. The one site dominated by woody vegetation was also removed, as it was both a mathematical and ecological outlier. These types of systems are ecologically different from the primary target population, and this is reflected by the vegetation attributes of these sites. The resulting metrics, therefore, are derived from herbaceous-dominated intermittent or ephemeral riverine wetlands.

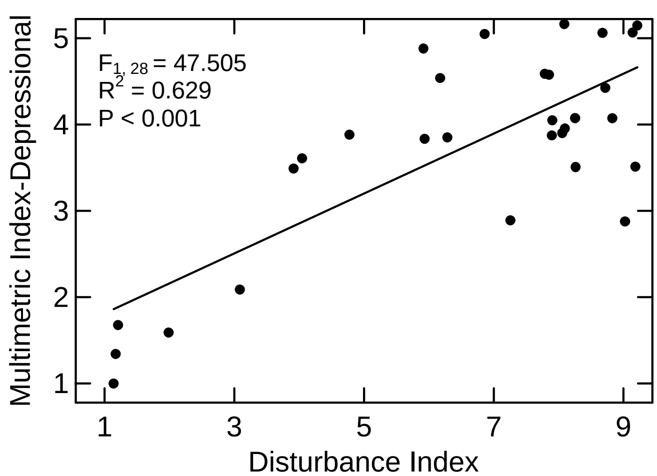

Figure 11. Relationship between multimetric index and site disturbance index for temporarily and seasonally flooded depressional wetlands (n = 30). Metrics include the relative cover of native perennials, relative cover of species with C-value ≥ 4, relative cover of exotic species, and floristic quality index.

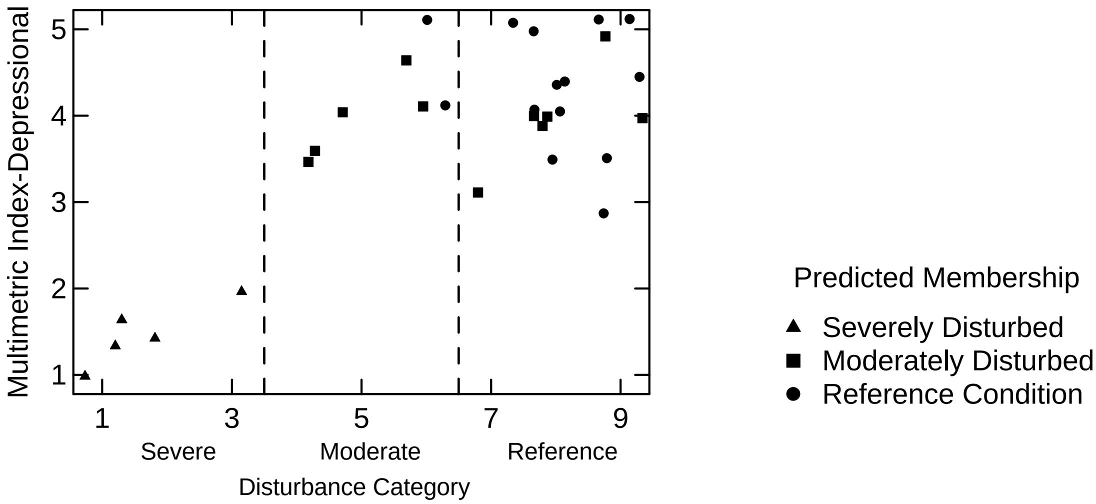

Figure 12. The predicted membership of temporarily and seasonally flooded depressional wetlands to disturbance categories compared with actual group membership. Predicted membership is based on discriminant analysis of vegetation metrics.

Metrics and the Multimetric Index

Thirteen of the 35 attributes examined exhibited a predictable response to human disturbance (Figure 14). Unfortunately, many of these attributes were biologically redundant. The first group of redundant attributes was total species richness, richness of native perennials, and richness of dicots. Of the 147 species sampled, 118 were native perennials and 100 were dicots; therefore, the species pools of these groups substantially overlapped. Additionally, these attributes were highly inter-correlated (total richness–richness of native perennials, r_s = 0.848; total richness–richness of dicots, r_s = 1.000; richness of native perennials–richness of dicots, r_s = 0.848). The richness of native perennials was the metric selected, as it was both the most highly correlated with disturbance and the most ecologically relevant. The second redundant group included the two diversity measures, Shannon and Simpson diversity. Although Shannon diversity was more strongly correlated with disturbance, Simpson diversity was chosen, as its properties were more appropriate to the vegetation sampling methodology used (see Results under Depressional Wetlands). Many attributes were derived from functional groups based on a species' C-value. These included richness of species with C-value ≥ 4, richness of species with C-value ≥ 5, and richness of intolerant species (C-value ≥ 6), as well as the relative cover of intolerant species and intolerant graminoids. All of these attributes were highly inter-correlated and shared many species in common. Although it was not the most highly correlated with disturbance, the relative cover of intolerant species was selected as a metric. It was chosen over the richness of species with C-value ≥ 4 and richness of species with a C-value ≥ 5, both of which had higher r_s values, because it was restricted to more disturbance-intolerant species and because cover is a more sensitive measure of species response than is presence-absence (Rahel 1990). The last redundant group was FQI and average C-value (r_s = 0.932). FQI was selected based on its higher correlation with disturbance.

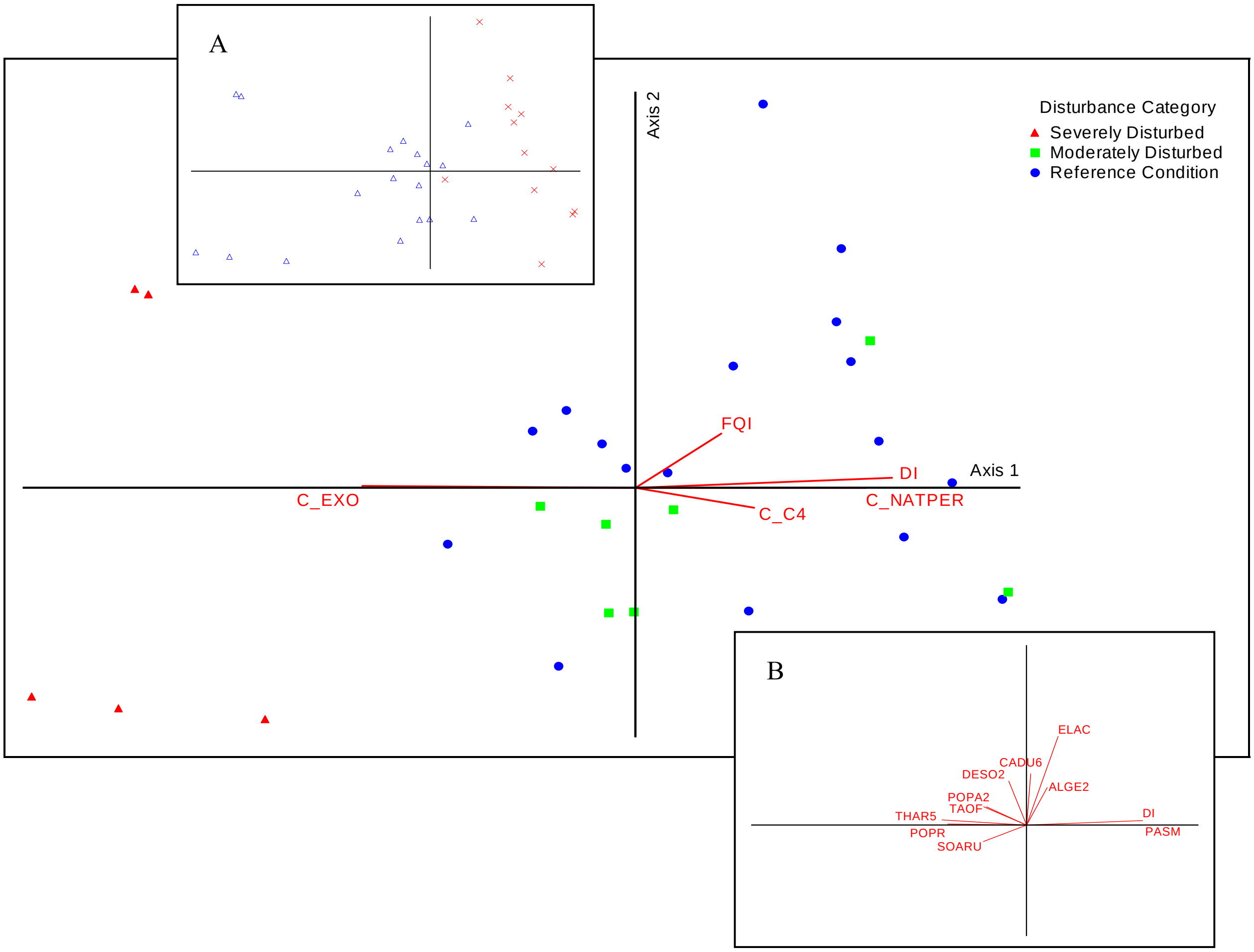

Figure 13. Graphical representation of the NMS ordination of sampled temporarily and seasonally flooded depressional wetlands. Points represent species cover and composition data for quadrats aggregated by site. Distance between points is proportional to dissimilarity between samples (i.e., samples with similar species composition are plotted closer together). Axis 1 represents 68.2% of the variation in the data while Axis 2 accounts for 14.1% (total variation explained = 82.3%). Axes were rotated such that Axis 1 corresponds to the human disturbance gradient. Vectors are joint plots of variables correlated with ordination scores. Vector lengths represent the strength of the correlation; all variables have an $R^2 > 0.20$. Vectors in the main graph represent vegetation metrics and the disturbance index; vectors in Inset B represent highly correlated indicator species. Labels are: (main graph) C_NATPER = relative cover of native perennials, C_C4 = relative cover of species with C-value ≥ 4, C_EXO = relative cover of exotic species, FQI = floristic quality index, DI = disturbance index; (Inset B) ALGE2 = *Alopecurus geniculatus*, CADU6 = *Carex duriuscula*, DESO2 = *Descurainia sophia*, ELAC = *Eleocharis acicularis*, PASM = *Pascopyrum smithii*, POPA2 = *Poa palustris*, POPR = *Poa pratensis*, SOARU = *Sonchus arvensis* ssp. *uliginosus*, TAOF = *Taraxacum officinale*, THAR5 = *Thlaspi arvense*, DI = disturbance index. DI values range from 1 (most disturbed) to 9 (least disturbed). Inset A shows the importance of inundation period to plant community composition. Symbols represent site hydrology: Δ = seasonally flooded wetlands, × = temporarily flooded wetlands.

Table 6. Species indicative of severely disturbed and reference condition temporarily or seasonally flooded depressional wetlands. Indicator and P-values were determined using indicator species analysis; species shown had an indicator value ≥ 20 and a P-value ≤ 0.1.

Species	Disturbance Category[1]	Indicator Value	P-value
Poa palustris	D	60.0	0.002
Poa pratensis	D	60.0	0.002
Thlaspi arvense	D	59.5	0.002
Rumex salicifolius	D	69.6	0.009
Convolvulus arvensis	D	40.0	0.021
Taraxacum officinale	D	73.8	0.026
Descurainia sophia	D	34.3	0.055
Sonchus arvensis ssp. *uliginosus*	D	36.6	0.063
Rumex crispus	D	31.0	0.093
Alopecurus geniculatus	R	51.4	0.033
Cryptantha torreyana	R	48.5	0.036
Pascopyrum smithii	R	49.6	0.044
Eleocharis acicularis	R	50.3	0.061
Veronica peregrina	R	41.7	0.062
Carex duriuscula	R	44.2	0.072

[1] D = severely disturbed, R = reference condition

Value ranges for selected metrics were calculated based on quantile plots. Value breaks for quantile plots were determined at the 33rd and 67th quantiles, with some variability based on natural breaks in the data or tied values. Metric value ranges are presented in Table 7. The resulting multimetric index was significantly related to human disturbance ($F_{1, 20}$ = 77.511, R^2 = 0.795, $P < 0.001$; Figure 15).

Similar to depressional wetlands, the disturbance index was divided into three disturbance categories. The overall ability of vegetation metrics to correctly classify sites with regard to disturbance category was 86%, with 7 out of 8 severely disturbed sites correctly classified, 7 out of 9 moderately disturbed sites correctly classified, and 5 out of 5 reference condition sites correctly classified (results based on discriminant analysis; Figure 16).

Vegetation Community Response

In contrast to the many vegetation attributes that showed a strong response to human disturbance, composition and abundance of the whole plant community sampled at a site was not predictably associated with disturbance category (MRPP, A = 0.016, P = 0.310). This lack of correspondence is graphically displayed in Figure 17 (NMS, three-dimensional solution, final stress = 12.373, instability = 0.00001, 139 iterations).

DISCUSSION

Vegetation metrics were successful in assessing condition of both depressional and riverine wetlands. Human disturbance, as measured by an integrative disturbance index, explained 63% of the variation in the multimetric index for depressional wetlands and 80% of the multimetric variation for riverine wetlands. Vegetation metrics were

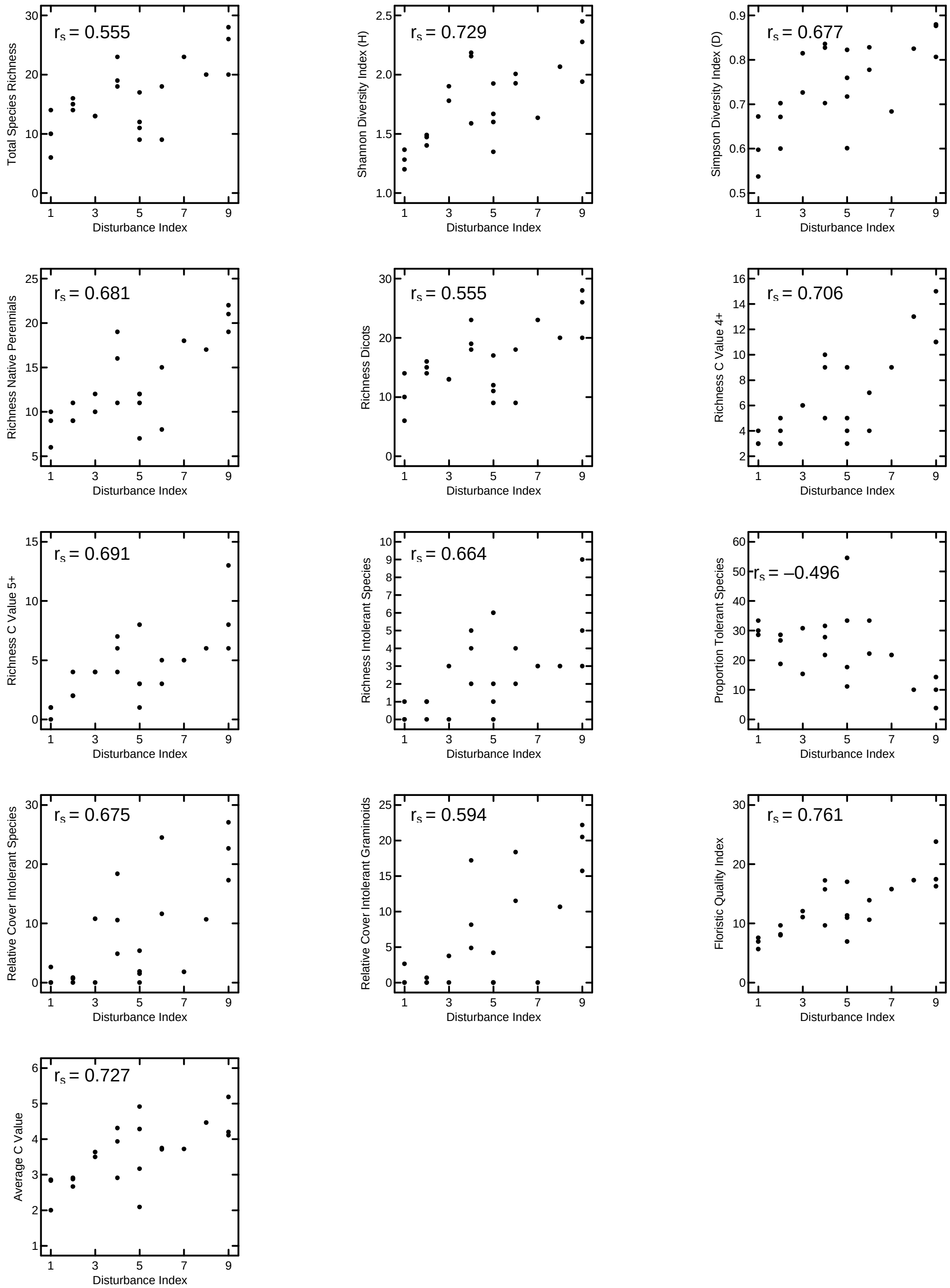

Figure 14. Scatter plots of attribute values against site disturbance index for herbaceous-dominated intermittent and ephemeral riverine wetlands. Shown are vegetation attributes that had a linear or curvilinear response to human disturbance and differentiated between least and most disturbed sites. Disturbance index ranges from 1 (most disturbed) to 9 (least disturbed). r_s = Spearman rank-order correlation coefficient.

Table 7. Ranges of attribute values for metric scoring categories for herbaceous-dominated intermittent and ephemeral riverine wetlands. Relative cover and proportionate richness values are expressed as percentages.

Metric	Value Range for 1	Value Range for 3	Value Range for 5
Richness of native perennials	< 11	11–14	≥ 15
Simpson diversity index	< 0.710	0.710–0.819	≥ 0.820
Relative cover of intolerant species	< 1.00	1.00–11.99	≥ 12.00
Proportionate richness of tolerant species	≥ 30.00	18.00–29.99	< 18.00
Floristic quality index	< 10.00	10.00–15.77	≥ 15.78

also able to correctly classify a wetland as either being severely disturbed, moderately disturbed, or in reference condition for 73% of depressional and 86% of riverine wetlands sampled.

The multimetric index for depressional wetlands was less robust than the riverine index, largely because it did not clearly differentiate between reference condition and moderately disturbed sites. While 100% of severely disturbed sites were correctly classified, only 71% of moderately disturbed and 67% of reference condition sites were correctly identified. This is likely due in part to the underlying response of some of the metrics to human disturbance. Two of the four metrics used, relative cover of species with C-value ≥ 4 and relative cover of exotic species, strongly responded to previous agricultural use in a wetland, but showed no response to other disturbance factors. In fact, only the FQI metric had a clearly linear response along the entire disturbance gradient.

The sensitivity of the multimetric index to agricultural disturbance is consistent with previous studies that have identified direct (i.e., wetland cropping) and indirect (i.e., adjacent land use) agricultural disturbances as important stressors of depressional

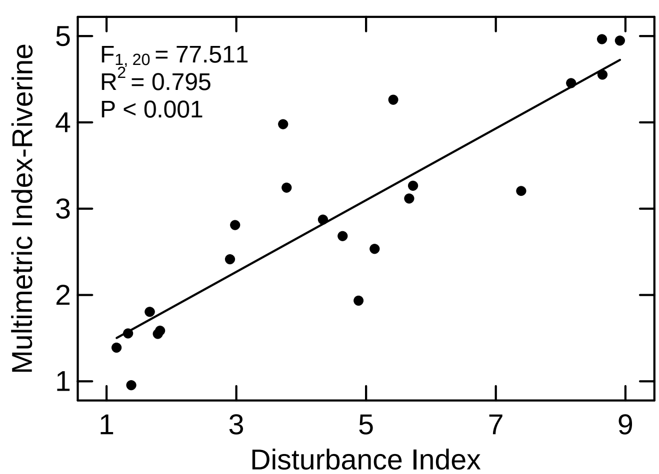

Figure 15. Relationship between multimetric index and site disturbance index for herbaceous-dominated intermittent and ephemeral riverine wetlands (n = 22). Metrics include the richness of native perennials, Simpson diversity index, relative cover of intolerant species, proportionate richness of tolerant species, and floristic quality index.

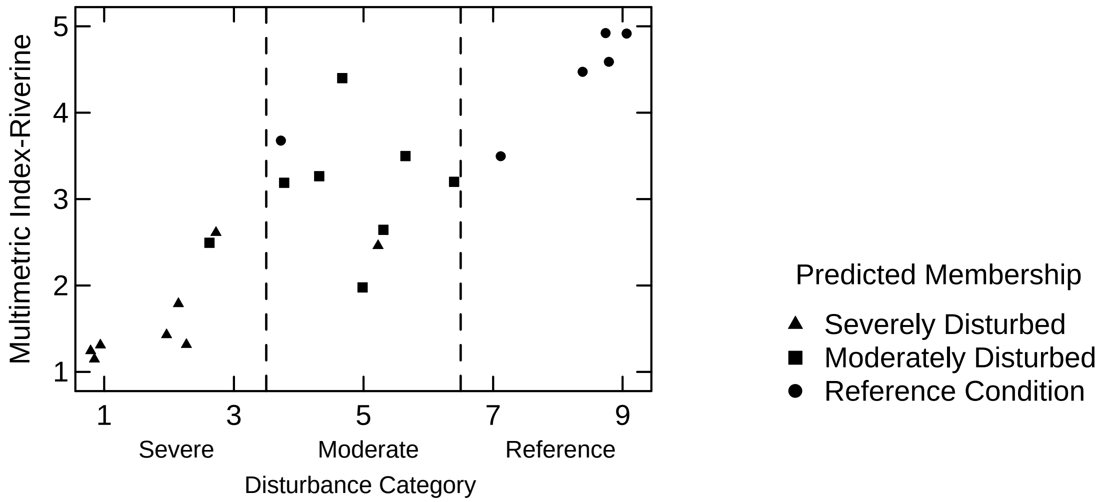

Figure 16. The predicted membership of herbaceous-dominated intermittent and ephemeral riverine wetlands to disturbance categories compared with actual group membership. Predicted membership is based on discriminant analysis of vegetation metrics.

wetlands in the prairie pothole region (Kantrud et al. 1989, Euliss and Mushet 1996, Kantrud and Newton 1996, Euliss and Mushet 1999, Freeland and Richardson 1999, Seabloom and van der Valk 2003). Unlike other disturbances, such as grazing, fire, or drought, wetland tilling can completely alter the species composition in a wetland. The effects of this conversion can persist even after cropping ceases and any concomitant hydrological alterations to the wetland have been restored (Galatowitsch and van der Valk 1996, Seabloom and van der Valk 2003). Given the magnitude of the disturbance, it is unsurprising that sites that had been previously tilled were so well differentiated by both metrics and NMS ordination. All species indicative of severely disturbed (i.e., previously tilled) sites were either invasive or weedy exotic species or native ruderals.

In contrast to agricultural disturbances, vegetation did not strongly respond to grazing-related stress. This may reflect vegetation adaptation to grazing pressure or inadequate sampling of heavily grazed sites. Prairie pothole vegetation developed in conjunction with American bison (*Bison bison*) and was subjected to intense short-term grazing pressure. Cattle, in contrast, tend to preferentially use wetter and more productive areas, leading to long duration, heavy use of these areas. Unlike riverine wetlands, the effects of this grazing pattern may be ameliorated in temporarily and seasonally flooded depressional wetlands due to their brief inundation periods.

The riverine multimetric model was better at assessing site condition across the entire human disturbance gradient, and was especially good at identifying the most and least disturbed sites (classification accuracy was 88% for severely disturbed wetlands and 100% for reference condition wetlands). Yet in contrast to the success of the multimetric index and unlike the results for the depressional dataset, whole-community analysis showed no relationship between vegetation and disturbance categories. The results of the multivariate analyses, however, were inconclusive not because vegetation did not change along a human distur-

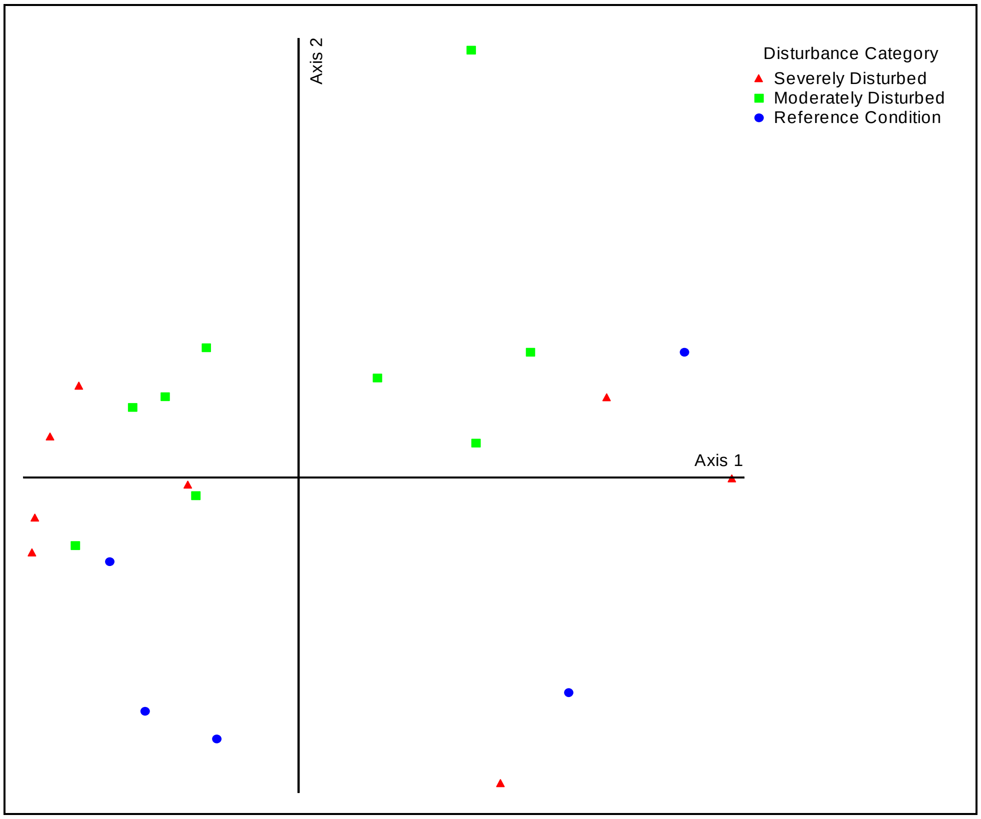

Figure 17. Graphical representation of the NMS ordination of sampled herbaceous-dominated intermittent and ephemeral riverine wetlands. Points represent species cover and composition for quadrats aggregated by site. Distance between points is proportional to dissimilarity between samples (i.e., samples with similar species composition are plotted closer together). Axis 1 represents 45.5% of the variation in the data and axis 2 accounts for 24.9% (total variation explained = 70.4%). Neither vegetation metrics nor the disturbance index were sufficiently correlated with ordination scores to be displayed as joint plots.

bance gradient, but because vegetation within disturbance categories was so variable. Even though the riverine wetland "reference domain" was restricted over the course of this study (i.e., the removal of perennial, alkaline, and woody-dominated wetlands), these wetlands still encompassed considerable environmental heterogeneity. Variation in species composition related to this environmental heterogeneity is reflected by the multiple vegetation assemblages representative of both reference and highly disturbed sties. For example, reference condition wetlands included sites along ephemeral streams dominated by tufted hairgrass and western wheatgrass as well as wetter sites along intermittent streams dominated by Nebraska sedge, common threesquare, and softstem bulrush (*Schoenoplectus tabernaemontani*). In contrast, depressional wetlands were consistently occupied by a relatively small suite of dominant species.

The superior ability of metrics to accurately classify wetland condition is due to the attributes used. While multivariate analyses examined the response of the whole plant community, vegetation metrics, with the exception of Shannon diversity, were based on plant functional groups. Functional groups classify plant species based on common attributes, adaptations, or responses to environmental factors (Runkiaer 1934, Grime 1977, 1988, McIntyre and Lavorel 1994, Lavorel et al. 1997). For example, classifications of wetland plants have been proposed based on shared functional or life-history traits, such as plant height, total leaf area, life span, propagule longevity and establishment requirements, and relative growth rate (van der Valk 1981, Boutin and Keddy 1993, Hills et al. 1994).

In this study, two types of functional groups were used, native perennials and species assemblages based on coefficient of conservatism values. Both of these factors have been shown to be responsive to disturbance. The index used to quantify human disturbance for riverine wetlands was primarily a measure of grazing intensity, and perennial species have been shown to respond negatively to grazing intensity in temperate grasslands in Australia (McIntyre et al. 1995). The C-values used in this study were subjectively assigned by an expert panel and represent a collective best professional judgment of a species' tolerance to disturbance and fidelity to habitat integrity (Northern Great Plains Floristic Quality Assessment Panel 2001). As such, C-values are an integrative measure of species response to a broad array of anthropogenic stressors. These panel-assigned C-values were good indicators of species response and fidelity and gave comparable results when compared to C-values derived from an independent dataset by Mushet et al. (2002) for prairie pothole wetlands in North Dakota. C-values and the resulting floristic quality index have been shown to be robust metrics in various wetland settings by Andreas and Lichvar (1995), DeKeyser (2000), and Lopez and Fennessy (2002).

Although the riverine multimetric index is relatively robust, it could be improved by defining additional functional groups based on shared species response to dominant stressors. For example, in the riverine systems evaluated, grazing is an important disturbance factor. Using metrics based on a grazing-sensitive functional group (for examples see McIntyre et al. 1995, Lavorel et al. 1997, Pausas and Lavorel 2003) could improve the biological sensitivity and overall accuracy of the multimetric index.

The multimetric indices developed for depressional and riverine wetlands are based on limited datasets. To validate and refine these tools, as well as evaluate their applicability to other ecoregions in the Great Plains, they should be tested in additional watersheds and in adjacent ecoregions. Prairie potholes are found primarily on glacial landforms and so are largely limited to the northwestern glaciated plains ecoregion of northern Montana. In contrast, the riverine multimetric model may have broad applicability to intermittent and ephemeral streams for much of eastern Montana.

Watershed disturbance rankings did not correlate with either small-scale disturbance measures or vegetation metrics, and this finding argues against the use of large-scale land use patterns as a surrogate for site-level measures of disturbance. In contrast, meso-scale land use variables, applied to a buffer area around a wetland or its upstream catchment, were shown to be meaningful components of a spatially integrative site disturbance index. Unfortunately, the effectiveness of the watershed ranking model was hampered by methodological problems: high multicollinearity and an unstandardized scoring base among variables. A refined ranking procedure may provide a more accurate measure of human disturbance at a 5^{th}-level watershed scale. Still, the applicability of such a model will be limited by the correspondence between large-scale land use measures and the dominant wetland stressor. For example, site-level grazing intensity is less likely to be correlated with watershed-scale land uses than is agricultural disturbance. Thus, a refined watershed disturbance rank procedure would likely be more useful as an indicator of wetland condition for depressional wetlands than riverine wetlands in the study area.

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APPENDIX A. SPECIES LISTS FOR DEPRESSIONAL AND RIVERINE WETLANDS

Table A. List of vascular plant species observed in temporarily and seasonally flooded depressional wetlands.

Scientific Name	Common Name	Growth Form[1]	Duration[2]	Nativity[3]
Achillea millefolium	common yarrow	F	P	N
Agropyron cristatum	crested wheatgrass	G	P	E
Agrostis scabra	rough bentgrass	G	P	N
Agrostis stolonifera	creeping bentgrass	G	P	E
Alopecurus geniculatus	water foxtail	G	P	E
Alopecurus pratensis	meadow foxtail	G	P	E
Argentina anserina	silverweed cinquefoil	F	P	N
Arnica fulgens	foothill arnica	F	P	N
Artemisia cana	silver sagebrush	S	P	N
Artemisia ludoviciana	white sagebrush	F	P	N
Atriplex argentea	silverscale saltbush	F	A/B	N
Beckmannia syzigachne	American sloughgrass	G	A/B	N
Bouteloua gracilis	blue grama	G	P	N
Bromus hordeaceus ssp. *hordeaceus*	soft brome	G	A/B	E
Bromus inermis	smooth brome	G	P	E
Bromus japonicus	Japanese brome	G	A/B	E
Carex atherodes	wheat sedge	G	P	N
Carex duriuscula	needleleaf sedge	G	P	N
Carex pellita	woolly sedge	G	P	N
Cerastium nutans	nodding chickweed	F	A/B	N
Chenopodium album	lambsquarters	F	A/B	E
Chenopodium spp.	goosefoot	F	A/B	E/N
Cirsium arvense	Canada thistle	F	P	E
Collomia linearis	tiny trumpet	F	A/B	N
Convolvulus arvensis	field bindweed	F	P	E
Cryptantha torreyana	Torrey's cryptantha	F	A/B	N
Deschampsia caespitosa	tufted hairgrass	G	P	N
Descurainia incana	mountain tansymustard	F	A/B	N
Descurainia sophia	herb sophia	F	A/B	E
Distichlis spicata	inland saltgrass	G	P	N
Eleocharis acicularis	needle spikerush	G	P	N
Eleocharis palustris	common spikerush	G	P	N
Elymus repens	quackgrass	G	P	E
Festuca spp.	fescue	G	P	N
Glaux maritima	sea milkwort	F	P	N
Gnaphalium palustre	western marsh cudweed	F	A/B	N
Grindelia squarrosa	curlycup gumweed	F	A/B	N
Hordeum jubatum	foxtail barley	G	P	N
Juncus balticus	Baltic rush	G	P	N

Scientific Name	Common Name	Growth Form[1]	Duration[2]	Nativity[3]
Koeleria macrantha	prairie junegrass	G	P	N
Lepidium densiflorum	common pepperweed	F	A/B	N
Leptochloa fusca ssp. *fascicularis*	bearded sprangletop	G	A/B	N
Medicago sativa	alfalfa	F	P	E
Mentha arvensis	wild mint	F	P	N
Muhlenbergia richardsonis	mat muhly	G	P	N
Myosurus apetalus	bristly mousetail	F	A/B	N
Navarretia intertexta	needleleaf navarretia	F	A/B	N
Opuntia polyacantha	plains pricklypear	S	P	N
Pascopyrum smithii	western wheatgrass	G	P	N
Penstemon spp.	beardtongue	F	P	N
Plagiobothrys scouleri	sleeping popcornflower	F	A/B	N
Plantago elongata	prairie plantain	F	A/B	N
Poa palustris	fowl bluegrass	G	P	N
Poa pratensis	Kentucky bluegrass	G	P	E
Poa secunda	Sandberg bluegrass	G	P	N
Polygonum spp.	knotweed	F	P	N
Polygonum ramosissimum	bushy knotweed	F	A/B	N
Puccinellia nuttalliana	Nuttall's alkaligrass	G	P	N
Ratibida columnifera	prairie coneflower	F	P	N
Rumex crispus	curly dock	F	P	E
Rumex spp.	dock	F	P	E/N
Rumex salicifolius	willow dock	F	P	N
Schedonnardus paniculatus	tumblegrass	G	P	N
Schoenoplectus pungens	common threesquare	G	P	N
Sonchus arvensis ssp. *uliginosus*	moist sowthistle	F	P	E
Taraxacum officinale	common dandelion	F	P	E
Thlaspi arvense	field pennycress	F	A/B	E
Tragopogon dubius	yellow salsify	F	A/B	E
Trifolium spp.	clover	F	P	E
Veronica peregrina	neckweed	F	A/B	N
Vicia americana	American vetch	F	P	N
Vulpia octoflora	sixweeks fescue	G	A/B	N

[1] F = forb, G = graminoid, S = shrub
[2] A/B = annual/biennial, P = perennial
[3] E = exotic, N = native

Table B. List of vascular plant species observed in intermittent and ephemeral riverine wetlands.

Scientific Name	Common Name	Growth Form[1]	Duration[2]	Nativity[3]
Achillea millefolium	common yarrow	F	P	N
Achnatherum nelsonii	Columbia needlegrass	G	P	N
Agoseris glauca	pale agoseris	F	P	N
Agropyron cristatum	crested wheatgrass	G	P	E
Agrostis scabra	rough bentgrass	G	P	N
Agrostis stolonifera	creeping bentgrass	G	P	E
Allium geyeri	Geyer's onion	F	P	N
Allium textile	textile onion	F	P	N
Alopecurus geniculatus	water foxtail	G	P	E
Antennaria microphylla	littleleaf pussytoes	F	P	N
Apocynum cannabinum	Indianhemp	F	P	N
Argentina anserina	silverweed cinquefoil	F	P	N
Artemisia cana	silver sagebrush	S	P	N
Artemisia frigida	prairie sagewort	S	P	N
Artemisia ludoviciana	white sagebrush	F	P	N
Atriplex argentea	silverscale saltbush	F	A/B	N
Beckmannia syzigachne	American sloughgrass	G	A/B	N
Bouteloua gracilis	blue grama	G	P	N
Bromus hordeaceus ssp. *hordeaceus*	soft brome	G	A/B	E
Bromus japonicus	Japanese brome	G	A/B	E
Calamagrostis stricta	northern reedgrass	G	P	N
Calamovilfa longifolia	prairie sandreed	G	P	N
Calystegia sepium	hedge false bindweed	F	P	N
Carex aquatilis	water sedge	G	P	N
Carex spp.	sedge	G	P	N
Carex nebrascensis	Nebraska sedge	G	P	N
Carex pellita	woolly sedge	G	P	N
Carex praegracilis	clustered field sedge	G	P	N
Chamaesyce serpyllifolia	thymeleaf sandmat	F	A/B	N
Chenopodium album	lambsquarters	F	A/B	E
Chenopodium spp.	goosefoot	F	A/B	E/N
Chenopodium pratericola	desert goosefoot	F	A/B	N
Cicuta douglasii	western water hemlock	F	P	N
Cirsium arvense	Canada thistle	F	P	E
Cirsium vulgare	bull thistle	F	A/B	E
Collomia linearis	tiny trumpet	F	A/B	N
Convolvulus arvensis	field bindweed	F	P	E
Conyza canadensis	Canadian horseweed	F	A/B	N
Danthonia spp.	oatgrass	G	P	N
Deschampsia caespitosa	tufted hairgrass	G	P	N
Descurainia sophia	herb sophia	F	A/B	E

Scientific Name	Common Name	Growth Form[1]	Duration[2]	Nativity[3]
Distichlis spicata	inland saltgrass	G	P	N
Downingia laeta	Great Basin calicoflower	F	A/B	N
Echinacea angustifolia	blacksamson echinacea	F	P	N
Echinochloa crus-galli	barnyardgrass	G	A/B	E
Eleocharis acicularis	needle spikerush	G	P	N
Eleocharis palustris	common spikerush	G	P	N
Elymus elymoides	squirreltail	G	P	N
Elymus repens	quackgrass	G	P	E
Elymus trachycaulus	slender wheatgrass	G	P	N
Epilobium spp.	willowherb	F	P	N
Epilobium pygmaeum	smooth spike-primrose	F	A/B	N
Equisetum arvense	field horsetail	F	P	N
Erigeron spp.	fleabane	F	P	N
Euphorbia esula	leafy spurge	F	P	E
Gaillardia aristata	common gaillardia	F	P	N
Galium boreale	northern bedstraw	F	P	N
Glaux maritima	sea milkwort	F	P	N
Glycyrrhiza lepidota	American licorice	F	P	N
Gnaphalium palustre	western marsh cudweed	F	A/B	N
Grindelia squarrosa	curlycup gumweed	F	A/B	N
Hackelia deflexa	nodding stickseed	F	A/B	N
Helianthella quinquenervis	fivenerve helianthella	F	P	N
Helianthella uniflora	oneflower helianthella	F	P	N
Helianthus annuus	common sunflower	F	A/B	N
Helianthus nuttallii	Nuttall's sunflower	F	P	N
Hesperostipa comata	needle and thread	G	P	N
Heterotheca villosa	hairy false goldenaster	F	P	N
Hieracium spp.	hawkweed	F	P	N
Hordeum jubatum	foxtail barley	G	P	N
Juncus balticus	Baltic rush	G	P	N
Juncus spp.	rush	G	P	N
Koeleria macrantha	prairie Junegrass	G	P	N
Lactuca serriola	prickly lettuce	F	A/B	E
Lemna minor	common duckweed	F	P	N
Lepidium densiflorum	common pepperweed	F	A/B	N
Lesquerella arenosa	Great Plains bladderpod	F	A/B	N
Linum lewisii	prairie flax	F	P	N
Lomatium spp.	desertparsley	F	P	N
Lycopus asper	rough bugleweed	F	P	N
Maianthemum stellatum	starry false lily of the valley	F	P	N
Medicago sativa	alfalfa	F	P	E
Mentha arvensis	wild mint	F	P	N
Muhlenbergia asperifolia	scratchgrass	G	P	N

Scientific Name	Common Name	Growth Form[1]	Duration[2]	Nativity[3]
Muhlenbergia richardsonis	mat muhly	G	P	N
Muhlenbergia spp.	muhly	G	P	N
Nassella viridula	green needlegrass	G	P	N
Navarretia intertexta	needleleaf navarretia	F	A/B	N
Opuntia polyacantha	plains pricklypear	S	P	N
Pascopyrum smithii	western wheatgrass	G	P	N
Pediomelum argophyllum	silverleaf Indian bread-root	F	P	N
Plantago elongata	prairie plantain	F	A/B	N
Plantago spp.	plantain	F	P	E
Plantago major	common plantain	F	P	E
Poa arida	plains bluegrass	G	P	N
Poa spp.	bluegrass	G	P	N
Poa palustris	fowl bluegrass	G	P	N
Poa pratensis	Kentucky bluegrass	G	P	E
Poa secunda	Sandberg bluegrass	G	P	N
Polygonum aviculare	prostrate knotweed	F	A/B	N
Polygonum erectum	erect knotweed	F	A/B	N
Polygonum spp.	knotweed	F	P	N
Polygonum ramosissimum	bushy knotweed	F	A/B	N
Potentilla gracilis	slender cinquefoil	F	P	N
Puccinellia nuttalliana	Nuttall's alkaligrass	G	P	N
Ranunculus cymbalaria	alkali buttercup	F	P	N
Ranunculus spp.	buttercup	F	A/B	N
Ratibida columnifera	prairie coneflower	F	P	N
Rhus trilobata	skunkbush sumac	S	P	N
Ribes aureum	golden currant	S	P	N
Rosa woodsii	Woods' rose	S	P	N
Rumex aquaticus	western dock	F	P	N
Rumex crispus	curly dock	F	P	E
Rumex spp.	dock	F	P	E/N
Rumex salicifolius	willow dock	F	P	N
Salix amygdaloides	peachleaf willow	T	P	N
Salix exigua	narrowleaf willow	S	P	N
Salix spp.	willow	S	P	N
Salsola tragus	prickly Russian thistle	F	A/B	E
Schoenoplectus maritimus	cosmopolitan bulrush	G	P	N
Schoenoplectus pungens	common threesquare	G	P	N
Schoenoplectus tabernaemontani	softstem bulrush	G	P	N
Selaginella densa	lesser spikemoss	F	P	N
Solidago spp.	goldenrod	F	P	N
Sonchus arvensis ssp. *uliginosus*	moist sowthistle	F	P	E
Spartina gracilis	alkali cordgrass	G	P	N
Spartina pectinata	prairie cordgrass	G	P	N

Scientific Name	Common Name	Growth Form[1]	Duration[2]	Nativity[3]
Stellaria spp.	starwort	F	A/B	N
Suaeda calceoliformis	Pursh seepweed	F	A/B	N
Symphoricarpos occidentalis	western snowberry	S	P	N
Symphyotrichum falcatum	white prairie aster	F	P	N
Symphyotrichum spathulatum	western mountain aster	F	P	N
Taraxacum officinale	common dandelion	F	P	E
Thermopsis rhombifolia	prairie thermopsis	F	P	N
Thlaspi arvense	field pennycress	F	A/B	E
Tragopogon dubius	yellow salsify	F	A/B	E
Trifolium spp.	clover	F	P	E
Trifolium repens	white clover	F	P	E
Triglochin maritimum	seaside arrowgrass	G	P	N
Typha latifolia	broadleaf cattail	F	P	N
Urtica dioica	stinging nettle	F	P	N
Veronica peregrina	neckweed	F	A/B	N
Vicia americana	American vetch	F	P	N
Viola spp.	violet	F	P	N
Xanthium strumarium	rough cockleburr	F	A/B	N
Zigadenus elegans	mountain deathcamas	F	P	N

[1] F = forb, G = graminoid, S = shrub, T = tree
[2] A/B = annual/biennial, P = perennial
[3] E = exotic, N = native

APPENDIX B. PHOTOGRAPHS OF SITES REPRESENTATIVE OF REFERENCE CONDITION, MODERATELY DISTURBED, AND SEVERELY DISTURBED WETLANDS

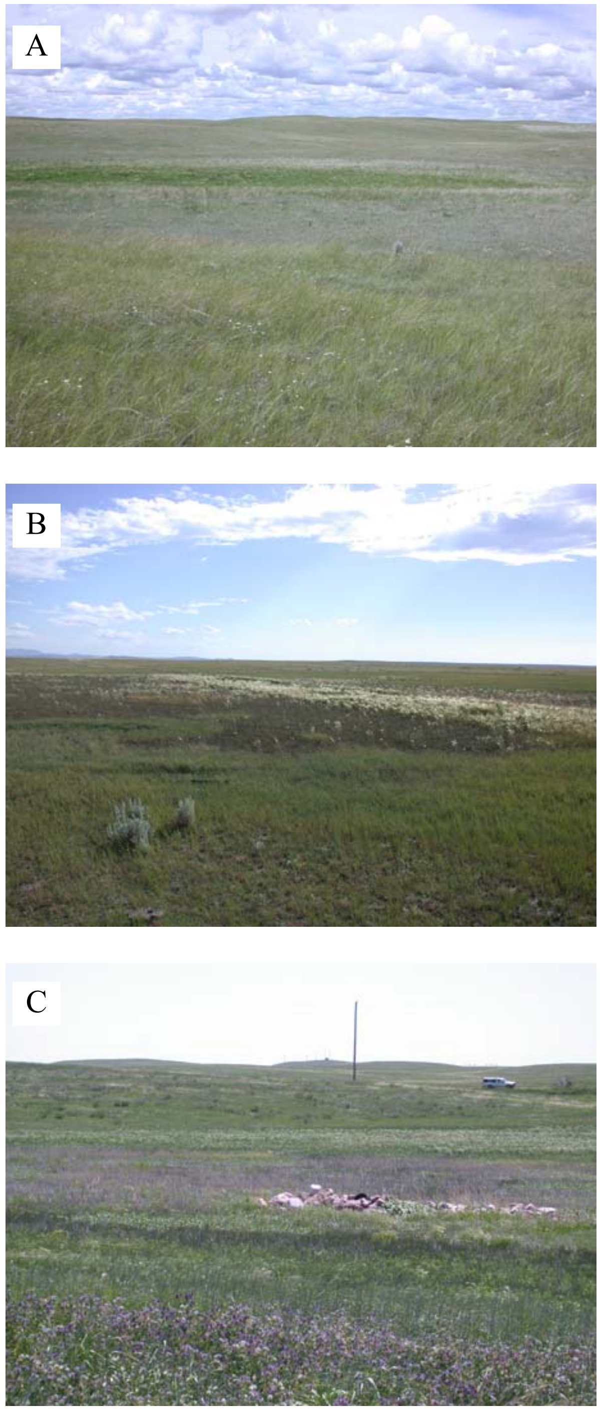

Figure A. Examples of (A) reference condition, (B) moderately disturbed, and (C) severely disturbed temporarily and seasonally flooded depressional wetlands.

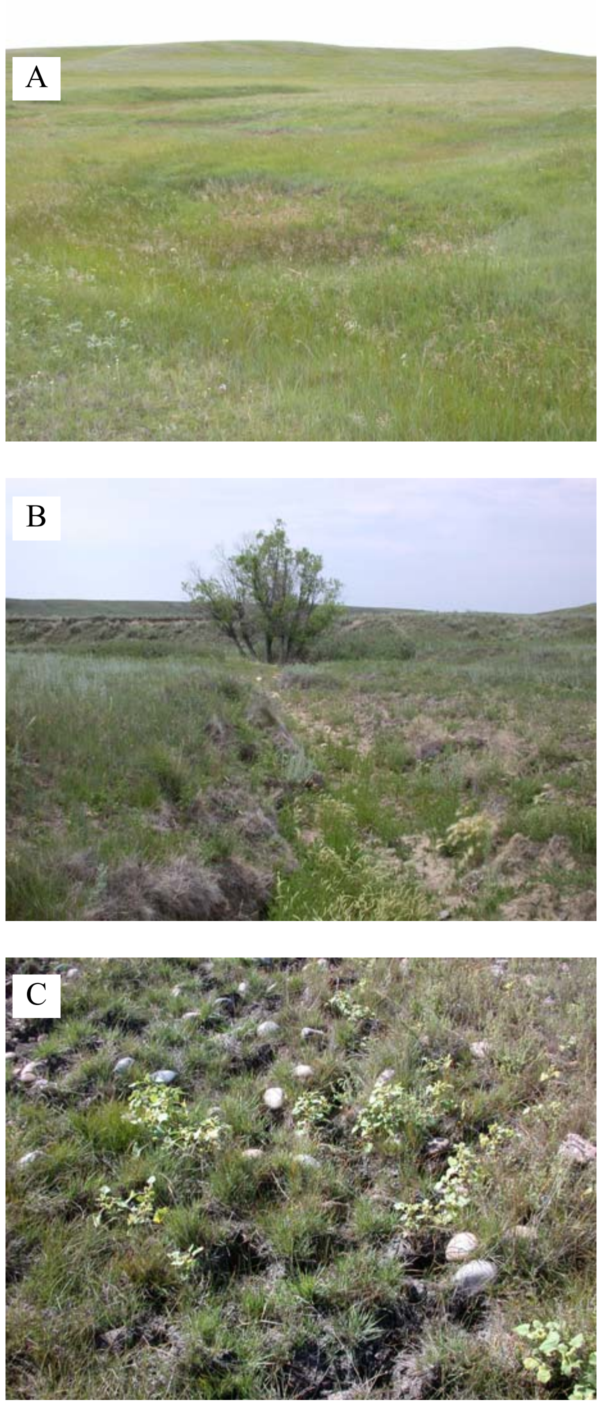

Figure B. Examples of (A) reference condition, (B) moderately disturbed, and (C) severely disturbed ephemeral riverine wetlands.

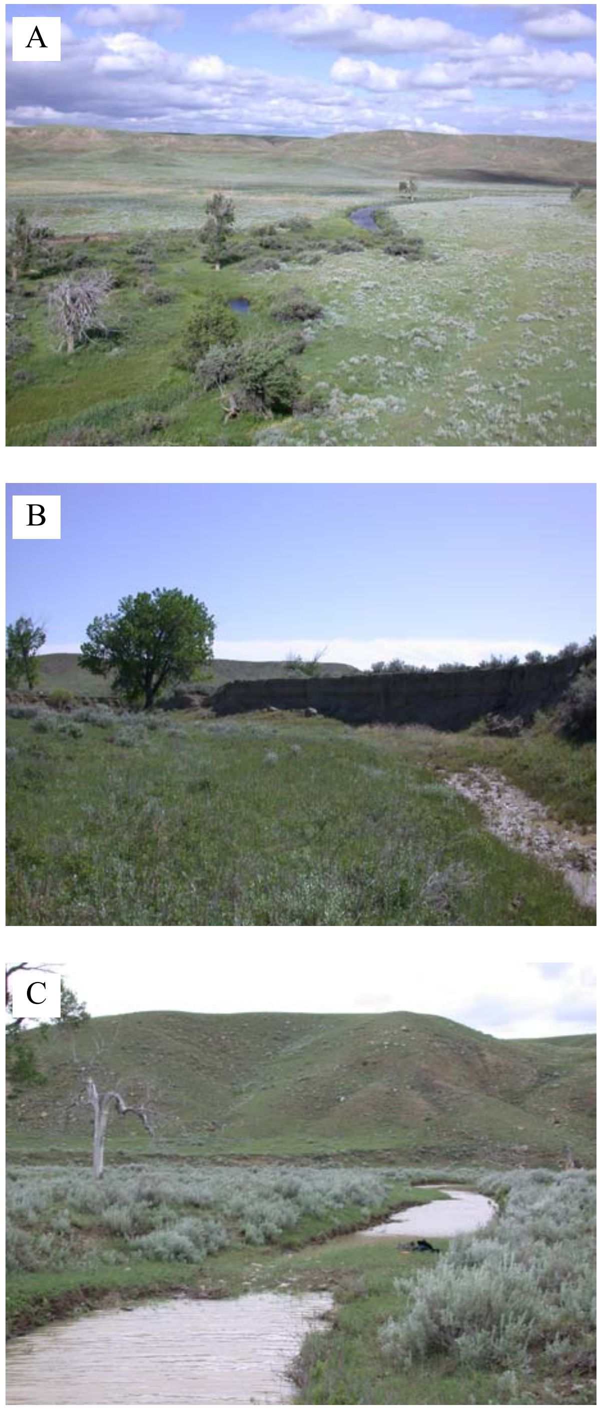

Figure C. Examples of (A) reference condition, (B) moderately disturbed, and (C) severely disturbed intermittent riverine wetlands.